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Effects of physical and chemical disturbance on stream ecosystem structure and function

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EFFECTS OF PHYSICAL AND CHEMICAL DISTURBANCE
ON STREAM ECOSYSTEM STRUCTURE AND FUNCTION

BY

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DISSERTATION

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In

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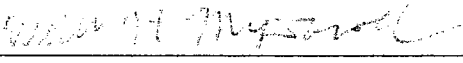
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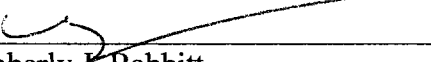


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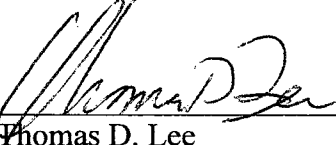
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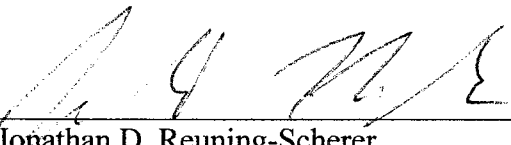
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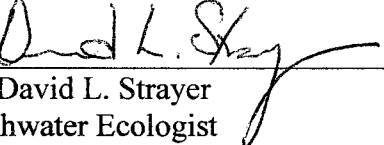
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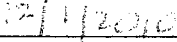
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ABSTRACT

EFFECTS OF PHYSICAL AND CHEMICAL DISTURBANCE ON STREAM ECOSYSTEM STRUCTURE AND FUNCTION

By

Elena Traister

University of New Hampshire, December, 2010

A variety of natural and anthropogenic disturbances influence the structure and function of stream ecosystems. While past investigations have focused on the response of community indicators to stream disturbances, functional indicators may also be helpful for assessing stream ecosystem health. To date, few studies have compared the response of structural and functional indicators to ecosystem-level disturbances. I separately measured the effects of long-term acidification, a large-scale avulsion, and the individual and combined effects of physical streambed disturbance and altered refugia availability on stream structural and functional metrics.

I found that acidification was associated with changes in macroinvertebrate communities including reduced diversity and reduced Ephemeroptera abundance. ^{13}C and ^{15}N isotopic signatures of three macroinvertebrate families shifted away from periphyton isotopic signatures and towards isotopic signatures of allochthonous food sources at acidified sites. Whole-stream metabolism was not significantly associated with stream pH and may be less sensitive to acidification than macroinvertebrate community metrics.

Following a large avulsion, I found that dramatically high levels of suspended sediment concentrations in and downstream of the avulsed channel recovered to background levels within approximately two months, and reduced substrate particle size in these areas were associated with reduced macroinvertebrate abundance, altered macroinvertebrate and fish communities, and reduced whole-stream respiration that persisted throughout the study period. Dewatering led to long-term changes in water chemistry, as well as changes to the fish community and reduced whole-stream respiration.

I found that increasing the frequency of streambed disturbance without altering stream substrate composition had minimal impact on macroinvertebrate and whole-stream metabolism metrics, however large streambed rocks appear to be very influential in maintaining stream ecosystem structure and function. The presence of refugium stones appears to be especially important in streams exposed to increased physical disturbance frequency.

These and other recent studies comparing the relative sensitivities of structural and functional metrics to environmental disturbance are a good first step towards being able to choose appropriate ecosystem metrics for different circumstances. However, to most effectively manage and monitor freshwater systems it is necessary to understand the mechanisms driving changes in ecosystem structure and function, and how these properties are linked.

INTRODUCTION

Background

A variety of natural and anthropogenic disturbances influences the structure and function of stream ecosystems. Natural variations in flow shape biotic communities by dislodging organisms and by altering stream geomorphology and the availability of food resources. Anthropogenic flow disturbances result from dams, diversions, and run-off from impervious surfaces. Human activities have also indirectly led to changes in flow through the intensification of the hydrologic cycle associated with climate change (IPCC 2007). In addition to altering flow, human activities result in a variety of other stream disturbances including sedimentation (resulting from construction, forestry, and agricultural practices), acidification (as a result of acid deposition), the introduction of non-native species, chemical and nutrient pollution, and channelization. Understanding these disturbances and their effect on stream ecosystem structure and function is central to developing successful stream conservation and restoration strategies.

Stream Disturbance and Recovery of Biotic Communities

Lake (2000) defined disturbance as occurring when, “potentially damaging forces are applied to habitat space occupied by a population, community, or ecosystem,” and he classified these disturbances into one of three categories based on their duration: pulses, presses, and ramps. “Pulses” encompass disturbances of short duration, such as floods.

“Presses”, including human-induced sedimentation and dewatering, exert long-term stress. “Ramps”, such as droughts, increase in intensity over time.

Yount and Niemi (1990) reviewed case studies documenting recovery of stream communities from disturbance. The authors found that recovery from a localized, short-term pulse disturbance is generally rapid (generally less than three years and frequently less than one year) for all taxa except fishes with long life cycles. They suggested several reasons for this rapid rate of recovery, including: 1) life history characteristics (short generation times, high fecundity, good dispersal ability); 2) availability of refugia from which organisms repopulate the reach following disturbance; 3) high flushing rates that dilute/remove pollutants; and 4) adaptation of stream biota to frequent disturbance.

Detenbeck et al. (1992) analyzed the same studies as reviewed by Yount and Niemi (1990) to determine the relative effects of autoecologic, site-specific, disturbance, and community structure factors on the recovery times of temperate stream fish following a disturbance. While community structure was not influential, all three other parameters (autoecologic, site-specific, and disturbance factors) played a role in determining how quickly stream fish communities would recover from a disturbance. For example, the authors identified characteristics of fish species that delay recovery (e.g. rock/nest-spawning guilds), properties of stream reaches that promote or delay recovery (e.g. refugia and barriers to migration, respectively), and characteristics of disturbances that delay recovery times (e.g. occurrence immediately after spawning). The authors also noted that there was little evidence of the influence of facilitative or inhibitory biotic interactions on recovery, leading them to conclude that competition and predation pressures are relaxed during recovery.

Monteith et al. (2005) proposed four hypotheses to explain the biotic response following chemical recovery of acidified surface waters in the UK. First, the relationship between the recovery of water chemistry and the response of biotic communities may be direct and linear. Alternatively, while the relationship between recovery of water chemistry and biotic response may be direct, the biota may exhibit a non-linear step-wise recovery in response to specific chemical thresholds. Their third hypothesis suggested that biotic communities respond to chemical recovery following time-lags due to dispersal limitation of acid-sensitive species into recovered waters. Finally, interspecific interactions may delay or prevent biological communities from fully recovering following chemical disturbance. For example, an acid-tolerant generalist species may take over the niche of a particular acid-sensitive specialist species, thereby preventing the reestablishment of the acid-sensitive species.

Functional Indicators of Stream Ecosystem Disturbance: Advantages

While past investigations have focused on the response of community indicators to stream disturbances, Young et al. (2008) have recently highlighted advantages of using functional indicators of stream ecosystem health such as leaf breakdown rate and whole-stream metabolism. For example, they noted that whole-stream metabolism measurements are more spatially integrative than community metrics, they may be carried out in as little as two days, and they provide information about the balance between energy supply and demand in streams. Furthermore, Bunn et al. wrote, “Many goals relating to river management and protection refer to ecosystem-level processes, with the notion that streams and rivers should function in the same way they do in

unimpacted catchments (1999).” Stream ecosystem function not only determines the base of lotic food webs, it also contributes to global carbon cycling (Cole et al. 2007), and to the uptake of nutrients responsible for the eutrophication of lakes and estuaries.

Several studies have documented situations in which anthropogenic disturbance to stream systems was reflected in functional metrics, but not in community metrics. For example, Bunn and Davies (2000) examined the response of stream metabolism and macroinvertebrate metrics to elevated nitrogen concentration and turbidity in small forest streams in southwest Australia. While macroinvertebrate metrics indicated no impairment, stream metabolism (GPP and R) varied markedly. In this case, while structural and functional metrics were not correlated, functional metrics were correlated with the source of water quality impairment.

Schultheis et al. (1997) investigated the effect of elevated copper levels on stream ecosystem structure and function downstream of a pyrite mine in Virginia. Initially, both community measures (macroinvertebrate abundance and taxa richness) and functional measures (leaf decomposition rate) were significantly impaired at the impacted sites. However, after six weeks of treating mine drainage to reduce metal concentrations and increase pH, community variables had recovered while decomposition rate remained impaired. Thus, while the functional metric was sensitive to residual effects of mine drainage in this case, community metrics failed to indicate any lingering impact.

Unfortunately, it is not always the case that anthropogenic disturbance is reflected in stream ecosystems by functional metrics; sometimes community metrics indicate disturbance when functional metrics do not. Nelson (2000) found significant differences among communities of macroinvertebrates inhabiting leaf packs above and below a

metals point source, while differences in decomposition rates of the leaf packs were not detected.

Functional Indicators of Stream Ecosystem Disturbance: Sensitivity

In order for a metric to be useful as an indicator of stream disturbance, it must be sufficiently sensitive to ecosystem perturbations. Schindler (1987) argued against using measures of ecosystem function because natural systems contain feedback mechanisms that buffer them against perturbation. In contrast, Gessner and Chauvet (2002) suggested that such concerns are based more on intuition than on facts from empirical work in streams. In fact, functional metrics have been shown to be sensitive to a variety of stream ecosystem disturbances including acidification, nutrient pollution, altered light availability, sedimentation, thermal pollution, geomorphic alteration, changes in flow, contamination with toxic substances, and changes in land cover, as discussed below.

Research examining the rates of leaf breakdown in streams has conclusively shown that acidification slows decomposition. As described by Rader et al. (1994), only four mechanisms directly determine the rate of leaf decomposition: (1) leaching; (2) microbial degradation; (3) macroinvertebrate fragmentation, and (4) flow-related fragmentation. Other factors may indirectly alter rates of decomposition by exerting an influence on one or more of these four (interrelated) processes. Leaves (particularly those of low palatability) are microbially conditioned (particularly by hyphomycete fungi) before being consumed by shredder macroinvertebrates. Therefore, reductions in leaf decomposition due to acidification could proceed by inhibiting fungal conditioning of the leaves and/or inhibiting the activity of shredders. Indeed, research has demonstrated that

depressed decomposition in acidified streams has sometimes been due to inhibition of microbial activity (Allard and Moreau 1986, Griffith and Perry 1994), and other times due to inhibition of shredder activity (particularly by eliminating the acid-sensitive shredder genus *Gammarus*) (Dangles and Guerold 2001, Dangles and Chauvet 2003).

While the effect of acidification on whole-stream metabolism has not yet been elucidated, the fact that acidification depresses microbial degradation of leaves in acidified streams (Chamier 1987) suggests that ecosystem respiration would likely be depressed at the scale of an entire stream reach. Additionally, several studies have documented declines in periphyton biomass within acidified streams (Vinyard 1996, Simmons et al. 2005), which suggests whole-stream GPP may also be depressed.

Elevated nutrient concentrations (particularly nitrogen and phosphorus) enhance microbial activity, thereby increasing the rate of leaf decomposition (see Menendez et al. 2003 for references). In a study of whole-ecosystem metabolism in eight streams from several biomes in North America, Mulholland et al. (2001) found that 90% of the variation in log GPP was explained by a multiple regression model including only streamwater soluble reactive phosphorus (SRP) concentration and log photosynthetically active radiation (PAR), while 73% of the variation in respiration was explained by a multiple regression model that included only SRP and size of the transient storage zone.

As the fundamental energy source for photosynthesis, light (and its obstruction) can control primary production in streams. As mentioned above, among streams of different biomes in North America, PAR was a strong predictor of whole-stream GPP (Mulholland et al. 2001). Exposure of the benthos to light can be limited in one of two main ways: shading by the riparian canopy, and turbidity, which results in light being

scattered and/or absorbed by fine sediment in the water column. Bott et al. (2006) found that GPP was higher in study sites with open riparian canopies as opposed to sites with greater riparian tree canopy density. While stream respiration is typically not controlled by light, Bunn et al. (1999) found that denser riparian vegetation depressed respiration along with GPP, which led them to conclude that benthic algae was responsible for a large part of ecosystem respiration in this system. Depression of GPP due to light obstruction has been documented due to turbidity (Wiley et al. 1990, Davies-Colley et al. 1992, Young and Huryn 1996, Young and Huryn 1999), as well as due to shading by a valley wall (Young and Huryn 1999).

In addition to blocking light to the benthos, fine sediments may also depress GPP. Suspended sediment in combination with increased water velocity has been shown to augment removal of periphyton biomass compared to that observed when velocity alone was increased (Francoeur and Biggs 2006). Horner et al. (1990) also documented a significant increase in periphyton loss rate when increased suspended sediment occurred in combination with greater velocity. When suspended sediment concentration was augmented in the absence of increased velocity, the periphyton loss rate was only marginally higher than under low suspended sediment conditions. Whether these changes to algal biomass are significant at the scale of entire stream reaches has yet to be demonstrated.

When fine sediments settle out of the water column, they can also depress rates of decomposition (Herbst 1980, Meyer 1980, Rader et al. 1994, Niyogi et al. 2003). Theoretically, this could be due to alteration of any one or more of the four mechanisms

outlined above: microbial degradation, macroinvertebrate fragmentation, leaching, and flow-related fragmentation.

Many studies in various stream systems, involving leaves of different types, have documented that higher temperatures result in more rapid decomposition, mainly by stimulating microbial processes (see Webster and Benfield 1986 for references). There is also evidence that higher temperatures lead to higher rates of whole-stream metabolism (Bott et al. 1985, Hedin 1990).

Studies have shown that ecosystem metabolism is responsive to several types of changes in stream geomorphology: substrate size, substrate stability, and substrate heterogeneity. Rier and King (1996) found significantly higher rates of net community productivity and community respiration in a cobble stream reach as compared with sandy reaches of the same stream. Houser et al. (2005) documented low and temporally variable whole-stream GPP in sandy-bottomed streams in which frequent resuspension and redistribution of sediments likely limited the development of primary producer communities. Cardinale et al. (2002) found that stream metabolism was reduced merely in response to increased uniformity of substrate size, likely due to changes in near-bed hydraulic conditions.

Several mechanisms could explain these differences in metabolism due to substrate size and stability. Altered near-bed hydraulics may change the supply rate of nutrients, gases, and organic matter to benthic microbial communities. Changes in hydraulics may also indirectly affect metabolism by altering microbial community composition. Stream metabolism may be depressed in stream reaches with unstable benthic sediments due to scouring, resuspension, and burial of periphyton. Sediment

instability has been shown to reduce periphyton biomass, with smaller, less stable sediments from lake inlet reaches supporting less periphyton biomass than more stable sediments from lake outlets (Myers et al. 2007). Studies have further documented greater variability of periphyton on unstable substrates, with flood events reducing epipsammic periphyton biomass more dramatically than epilithic periphyton biomass, and with epilithic periphyton biomass quicker to recover following spates (Uehlinger, 1991, Dodds et al. 1996).

Changes in flow can scour detritus and benthic organisms as well as attenuate light penetration by regulating water depth and turbidity (Uehlinger and Naegeli 1998, Uehlinger 2006). These changes tend to depress both ecosystem respiration (slightly) (Uehlinger and Naegeli 1998) and GPP (to a greater extent) (Young and Huryn 1996, Uehlinger and Naegeli 1998), thereby shifting the metabolic balance towards heterotrophy during spates.

Toxic substances, particularly metals and pesticides, appear to inhibit decomposition as well as whole-stream metabolism. However, these effects have mainly been noted only at very high concentrations of pollution (see Young et al. 2008 for references).

Urbanization and agriculture are indirectly linked to stream ecosystem function through a variety of pathways. Surface runoff from agricultural fields and impervious surfaces in urbanizing watersheds increases inputs of nutrients, sediment, and toxic substances to streams. Precipitation may be more acidic in urban areas, due to the release of nitrogen and sulfur oxides in vehicle exhaust. Deforestation of riparian buffer zones in urban and agricultural settings can increase exposure of the benthos to light,

channelization can directly affect stream geomorphology, and both may alter temperature regimes. As described above, each of these changes is potentially capable of altering stream ecosystem function directly and/or indirectly.

Chadwick et al. (2006) found that as watershed total impervious area (TIA) increased to 30-40%, leaf litter decomposition increased, but decomposition decreased when TIA was greater than 40%. They found that flow regime, snail biomass, invertebrate richness, and metal and nutrient content were significant predictors of litter breakdown rates in these streams. Meyer et al. (2005) also found that leaf litter decomposition was positively correlated with the percent of the catchment covered by high-intensity urban development.

Houser et al. (2005) found that watershed disturbance (indicated by areas of bare ground in the catchment) depressed ecosystem respiration. This effect was attributed to the development of unstable stream bottom sediments and high TSS during storms in disturbed sites, which buried coarse woody debris and other organic matter. Young and Huryn (1999) documented depressed GPP in a stream draining a catchment dominated by agricultural landcover, likely due to high turbidity levels blocking light to the benthos. On the other hand, Bunn et al. (1999) documented that increased crop/pasture land in the catchment led to higher rates of GPP and CR. In this case, the complementary effects of increased light and/or nutrient levels associated with agricultural land use may have overshadowed the negative effects of turbidity on whole-stream metabolism. Bott (2006) found that GPP, CR, as well as GPP/CR were negatively correlated with indices of urbanization including population density, residential land use, and several molecular tracers and hydrocarbons, while these parameters were positively correlated with forest

cover. While Meyer et al. (2005) did not find GPP, CR, or net ecosystem production to be correlated with indicators of urbanization, they did find that NH_4 and soluble reactive P uptake velocities decreased as high intensity urban development in the watershed increased. Furthermore, NH_4 uptake velocity increased with total stream metabolism (GPP + CR) in the study streams as well as in other North American streams, suggesting that biotic demand drives NH_4 uptake velocities across a wide range of stream ecosystems.

Comparing Structural and Functional Metrics of Stream Ecosystem Disturbance

Community metrics have thus far not been demonstrated to be good indicators of ecosystem function, though many studies investigate stream ecosystem function indirectly by examining macroinvertebrate functional feeding group dynamics. The extent to which functional feeding group dynamics reflect processes occurring at the reach scale is unknown. However, the potential problems with this approach are apparent if we consider an example concerning leaf litter decomposition. As described above, leaf litter decomposition rates can be altered by changes to one or more of the following four processes: leaching, microbial processing, macroinvertebrate processing, and physical abrasion. Therefore, when macroinvertebrate shredders most strongly control decomposition rates, reduction of macroinvertebrate shredder populations should depress litter decomposition rates. However, as described above, changes in temperature and fine sediment concentrations alter rates of decomposition mainly by altering rates of microbial processing, and this is often the case for acidification as well. Changes in

macroinvertebrate shredder communities would therefore be a poor choice for an indicator of altered decomposition rates under these circumstances.

While community metrics have not been demonstrated to be good indicators of ecosystem function, ecosystem function measures *have* been shown to be predictive of other ecosystem function metrics, as demonstrated above by the concordance between NH_4 uptake velocity and total stream metabolism. Thus, information regarding several whole-ecosystem processes may be obtained from relatively non-labor intensive measures of ecosystem function such as metabolism.

On the other hand, stream disturbances can affect ecosystem processes through several mechanisms, which may result in complementary effects on functional metrics that cancel each other out. For example, agricultural streams often exhibit elevated levels of turbidity (which depress GPP) along with increased nutrient concentrations and light exposure (which increase GPP). And while functional measures are comprised of a very limited number of parameters (decomposition rate, GPP, CR, and a few ways of combining GPP and CR), data from community studies are better suited for statistical ordination techniques that may better indicate relationships with environmental variables.

As discussed above, sometimes ecosystem disturbance is reflected only by community metrics, while at other times only by functional metrics; to date, theory and empirical studies offer little guidance as to which will be the case *a priori*. Schindler (1987) wrote, “Few single ecosystem-level studies of perturbation have incorporated a broad variety of organizational, nutrient-cycling, and energy-flow aspects; thus it is impossible to compare them.” Despite advances in ecological understanding over the past 20 years, this is still true today.

To address this deficiency, the three studies presented in the following chapters all document the response of both structural and functional indicators to ecosystem-level disturbances. Chapter 1 investigates long-term effects of acidification (a press disturbance) on macroinvertebrate communities and whole-stream metabolism. Chapter 2 reports on the effects of a large-scale avulsion on stream geomorphology, water quality, biotic communities, and whole-stream metabolism. This avulsion was associated with temporarily elevated flow and suspended solids (pulse disturbances), as well as persistent sedimentation and dewatering (press disturbances). Chapter 3 examines the individual and combined effects of physical streambed disturbance and altered refugia availability (both press disturbances) on macroinvertebrate communities and whole-stream metabolism.

CHAPTER 1

PERSISTENT EFFECTS OF ACIDIFICATION ON STREAM ECOSYSTEMS IN THE GEOMON NETWORK, CZECH REPUBLIC

Abstract

Acidification of surface water is a persistent threat to aquatic ecosystems throughout the world. In nine small streams ranging in pH from 4.0 to 7.7 and belonging to the GEOMON Network in the Czech Republic, I examined the long-term effects of acidification on macroinvertebrate communities, macroinvertebrate diet, and whole-stream metabolism. Acidification was associated with changes in macroinvertebrate communities including reduced diversity and reduced Ephemeroptera abundance. ^{13}C and ^{15}N isotopic signatures of three macroinvertebrate families shifted away from periphyton isotopic signatures and towards isotopic signatures of allochthonous food sources at acidified sites. Whole-stream metabolism was not significantly associated with stream pH and may be less sensitive to acidification than macroinvertebrate community metrics.

Introduction

Atmospheric transport and deposition of sulfuric and nitric acids has resulted in acidification of surface waters throughout large areas of the Northeastern United States, Canada, and Europe (Schindler 1988), and is a growing problem in China (Streets et al.

2001). The Clean Air Act in the United States, the Eastern Canada Acid Rain Program in Canada, and the Convention on Long-Range Transboundary Air Pollution and the Gothenburg Protocol in Europe, have lead to reductions in emissions of acidifying gases and limited recovery of surface water quality over the past three decades. Throughout eastern North America and Europe, surface water concentrations of sulfate are declining and modest gains in acid neutralizing capacity and Gran alkalinity have been documented, though nitrate concentrations have generally remained constant and widespread recovery of pH has lagged (Skjelkvale et al. 2005).

Continued recovery of acidified waters may be hampered by several factors. Although declines in sulfate concentrations in surface waters have been pronounced, they have not matched reductions in sulfate deposition, suggesting that soil processes may partially buffer these reductions in sulfate deposition (Skjelkvale et al. 2005). Declines in sulfate concentrations have also been accompanied by increases in dissolved organic carbon (DOC) due to reductions in ionic strength (Hruska et al. 2009). In turn, these increases in DOC (and component organic acids) may partially offset reductions in sulfate acidity (Evans et al. 2008). Climate change may also hinder recovery from acidification in several ways including more frequent and severe droughts, increased turnover of organic carbon, and increased mineralization of nitrogen (Skjelkvale et al. 2003). Models suggest that, while surface waters will continue to recover from acidification, international policies currently are not stringent enough to result in full recovery of surface waters in Europe and eastern North America (Wright et al. 2005).

Deterioration of water chemistry in acidified streams is accompanied by changes in benthic communities and aquatic ecosystem function. The effect of stream

acidification on benthic invertebrates has been studied extensively. Acidification consistently leads to reduced macroinvertebrate diversity, with sensitive taxa in the orders Plecoptera, Trichoptera, and particularly Ephemeroptera generally exhibiting reductions in abundance; see Hall et al. (1987) for references. The effect of acidification on whole-stream metabolism is poorly documented. Although several studies have found increased periphyton biomass in acidified streams (Mulholland et al. 1986, Junger and Planas 1993), other studies of acidified streams have found reduced periphyton biomass (Vinyard 1996, Simmons et al. 2005). Microbial decomposition (Groom and Hildrew 1989) and leaf litter processing rates (Griffith and Perry 1993) are generally reduced in streams of low pH.

These changes in ecosystem function in acidified streams have been postulated to lead to (through bottom-up control), as well as result from (through top-down control), changes in benthic communities and lotic food webs. The loss of scraper/grazer macroinvertebrates and concurrent increases in periphyton biomass documented in acidified streams have led to the hypothesis that loss of herbivory leads to increased primary production in acid streams where periphyton biomass is controlled by top-down processes (Mulholland et al. 1986, Niyogi et al. 2002). An alternative top-down hypothesis, based on the idea that macroinvertebrate feeding is more plastic than represented by functional feeding groups (Dangles 2002), suggests that herbivory is reduced in acidified streams because specialist scraper/grazer macroinvertebrates are replaced by generalists in this guild that do not rely exclusively on periphyton (Ledger and Hildrew 2005). Similarly, Dangles (2002) suggested that replacement of specialist shredders by generalist shredders leads to the reduced leaf litter processing rates

documented in acid streams. Bottom-up hypotheses for the shift toward allochthony in acidified streams have been proposed by Junger and Planas (1993), who suggested that periphyton taxa are replaced by those that are less palatable to macroinvertebrate consumers, and Groom and Hildrew (1989), who suggested that an increase in leaf litter (despite its poorer quality) favors macroinvertebrate shredders.

Given the widespread and long-lasting threat acid deposition poses to aquatic systems, along with the sparse documentation on how ecosystem function and lotic food webs respond to this disturbance, I aim to document how stream ecosystems in the Czech Republic continue to be affected by acidification. Specifically, this study focuses on nine streams along an acidification gradient and aims to detail (a) changes in macroinvertebrate communities, (b) changes in whole-stream metabolism, (c) whether whole-stream metabolism is as sensitive an indicator of acidification as is benthic community structure, and (d) changes in stream food webs.

Methods

The GEOMON network was established by the Czech Geological Survey (CGS) in 1993 to monitor elemental fluxes in 14 small forested catchments throughout the Czech Republic (Fottova 1995). The sites represent a wide range of acidification, with average pH values (as measured in this study) ranging from 4.0 to 7.7; see Fottova and Skorepova (1998) for a description of regional emission burdens, bedrock geology, and vegetation cover at GEOMON sites. Acidification of GEOMON sites varies primarily due to location downwind from coal-burning power plants and watershed bedrock composition. For example, two GEOMON sites located only 7 km apart from one another

and having similar acidic atmospheric deposition were found to differ dramatically in streamwater pH (3.87 vs. 7.25) due to differences in bedrock geology (slow-weathering leucocratic granite vs. ultramafic serpentinite, respectively) (Kram and Hruska 1994). Following the implementation between 1996 and 1998 of a desulfurization program in the Czech Republic, sulfur deposition declined dramatically in the northwest region of the country while nitrogen deposition increased over the same period (Fottova 2003). At the most acidified GEOMON site, streamwater SO_4 concentration declined from 568 $\mu\text{eq/L}$ in 1990 to 232 $\mu\text{eq/L}$ in 2000, however streamwater pH only increased from 3.92 to 4.07 over this time period (Hruska et al. 2002).

Nine representative GEOMON sites were selected for this study (Table 1.1), and field sampling was carried out during the summer of 2007. At each site, a 100-m reach was established immediately upstream of the GEOMON weir or as close as possible to the weir avoiding tributaries and culverts. Average stream width and depth were determined by establishing transects every 10 meters along each reach. Stratified Wolman (1954) pebble counts (Kondolf 1997) were carried out to characterize coarse surface substrate. Intermediate axes were measured using a hand-held gravel analyzer (Gravelometer, US SAH-97, Wildlife Supply Company, Buffalo, NY) for at least 100 particles. PAR was monitored at one streamside location in each reach during the period of oxygen measurements. Temperature and pH were logged at 5-minute intervals at the upstream end of each reach simultaneous with the measurement of stream metabolism. Streamwater samples were filtered in the field using pre-combusted glass fiber filters (0.7 μM pore size), and frozen until analysis at the University of New Hampshire (UNH) or CGS. Cation (Na^+ , K^+ , Ca^{2+} , and Mg^{2+}), and anion (NO_3^- , Cl^- , SO_4^{2-} , and F^-)

concentrations were measured using ion chromatography. Standard colorimetric were used to measure concentrations of ammonium (EPA 1983b) and phosphate (EPA 1983a).

Benthic macroinvertebrates were collected using a handheld net (approximately 28 cm in diameter and with a mesh size of 500 μm) and by scrubbing all rocks and disturbing sediment within 30 cm of the net frame. Within each 100-m reach, three replicate samples were collected from each major habitat type (pool, riffle, and run), for a total of 9 samples per site. Specimens were identified to the family level (except for Oligochaeta and Turbellaria, which were identified to class) in the field and then frozen for isotopic analysis. Macroinvertebrate community data were pooled by site for this investigation.

Table 1.1. Sample site characteristics; pH values were averaged over the course of stream metabolism measurements; watershed area data are from Kram et al. (2008).

Site	pH	Watershed Area (ha)
Anenský potok (ANE; previously GEM)	7.1	27
Jezeří (JEZ)	6.4	261
Na lizu (LIZ)	7.0	99
Loukov (LKV)	5.5	66
Lysina (LYS)	4.0	27
Pluhův bor (PLB)	7.7	22
Salačova Lhota (SAL)	7.3	168
Spálenec (SPA)	6.6	53
U dvou louček (UDL)	6.0	33

Whole stream metabolism was determined using a 1-station diurnal O_2 curve approach (Houser et al. 2005). Dissolved oxygen concentrations were logged at 5-minute

intervals at the upstream end of each 100-m reach for at least 24 hours. Reaeration coefficients, stream velocity, and discharge were determined based on the decline of dissolved propane concentration during a simultaneous, continuous injection of propane and NaCl (a conservative tracer) over each 100-m reach. At one site (ANE), propane was not detected at the downstream end of the reach. For this site, reaeration was estimated based on the linear relationship between log-transformed stream width and log-transformed reaeration rates for the other streams in this study. The change in dissolved oxygen concentration over 5-minute intervals was corrected for air-water O₂ exchange and then used to determine the net rate of dissolved oxygen change due to ecosystem metabolism over this interval. The rate of air-water O₂ exchange was calculated with the reaeration coefficient adjusted to the measured water temperature and logged % dissolved oxygen saturation. Nighttime respiration (R) was calculated as the sum of net ecosystem metabolism occurring at night, and daytime R was estimated as average nighttime R. Total daily R was calculated as the sum of nighttime and daytime R rates over 24 hours (midnight to midnight), and daily gross primary production (GPP) was calculated as the sum of the differences between estimated daytime respiration rates and net ecosystem metabolism. P/R was calculated as the ratio of GPP to R. All stream metabolism measurements took place during periods of base flow during the summer in order to avoid variability associated with storm flow.

Stable isotope analysis was used to determine the influence of pH on the relative contribution of food sources to macroinvertebrate diets. Food sources were collected by hand and included live and senesced leaves collected from riparian vegetation, epilithic periphyton scraped from rocks, coarse particulate organic matter (CPOM) including

leaves and twigs collected from the stream bottom, and fine particulate organic matter (FPOM) aspirated from the stream bottom using a baster. Benthic macroinvertebrates were collected as described above. The three most abundant macroinvertebrate families (Chironomidae, Leuctridae, and Nemouridae), which were found at all nine sampling locations, were analyzed for isotopic composition. Samples of macroinvertebrates and their food sources were frozen until prepared for analysis, at which point they were oven-dried at 60 °C for 36-48 h. Leaves and CPOM were pulverized for analysis. Periphyton and FPOM slurries were filtered through pre-combusted glass fiber filters (with a pore size of 0.45 µm), and residues were removed from filters for analysis. Whole macroinvertebrates from the same family and habitat (riffle, pool, or run) were pooled to obtain samples of sufficient mass. Samples were analyzed with isotope ratio mass spectrometers at the Czech Geological Survey and the University of New Hampshire Stable Isotope Laboratory. Stable isotope ratios are reported using δ notation as the difference in parts per thousand (‰) between the isotope ratio of the sample and that of a standard as follows:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}] \times 1000$$

$$R = {}^{13}\text{C}/{}^{12}\text{C} \text{ or } {}^{15}\text{N}/{}^{14}\text{N}$$

The standards used were PeeDee Belemnite formation for C and atmospheric nitrogen for N.

Linear regression was used to examine associations between pH and macroinvertebrate metrics and between whole-stream metabolism and water chemistry parameters. Macroinvertebrate abundance data were log-transformed ($\ln[1 + \text{abundance}]$) for these analyses. For each regression, influential observations were determined using Cook's (1977) distance. Statistically significant relationships at the 95% confidence level that were not significant when observations having Cook's distance >1 were removed from the analysis were not considered generally significant.

A general linear model was used to test whether pH was a significant predictor of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of macroinvertebrate food sources. MANOVA followed by multivariate contrasts was used to test for significant differences in isotopic composition among macroinvertebrate food sources. A general linear model was used to identify significant relationships between macroinvertebrate isotopic values and pH, habitat, and family membership.

Results

Kram et al. (2008) documented macroinvertebrate data collected at all nine GEOMON sites examined in this study. As shown in Figure 1.1, total macroinvertebrate family richness was associated with pH, with the largest number of families found at circumneutral sites ($R^2 = 82.9\%$; $t_7 = 5.82$; $p = 0.001$). Total macroinvertebrate abundance was not significantly associated with pH ($t_7 = -1.77$; $p = 0.120$). I tried fitting a multivariate model using pH to predict family richness and abundance simultaneously, but there was no evidence that it was any more powerful than looking at one variable at a time.

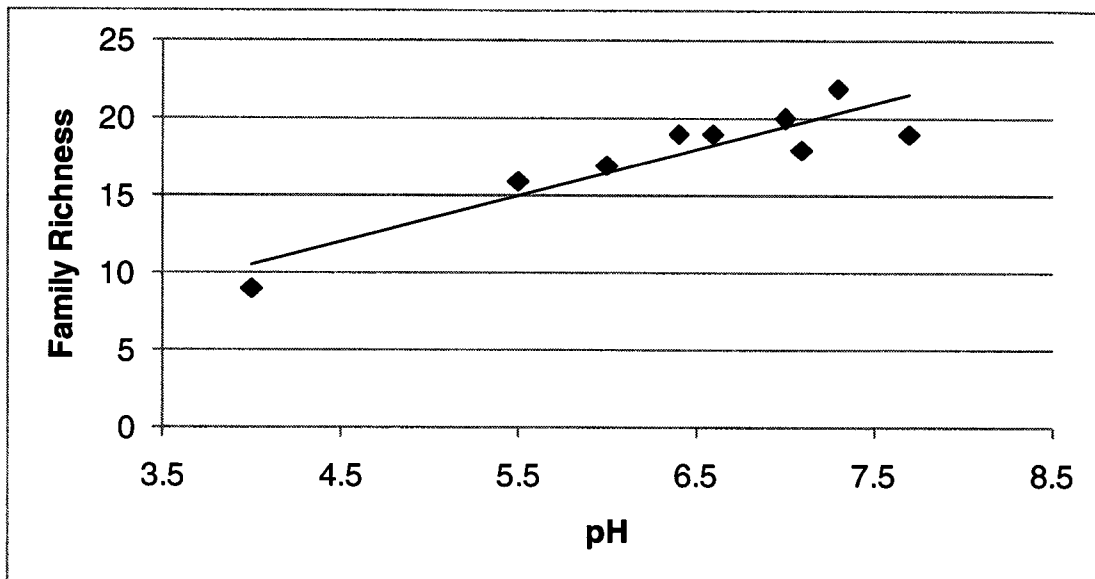


Figure 1.1. Relationship between macroinvertebrate family richness and pH

Mayflies exhibited pronounced sensitivity to acidification, and no Ephemeroptera families were found at the two most acidified sites. Ephemeroptera family richness was associated with pH (Figure 1.2a; $R^2 = 50.5\%$; $t_7 = 2.67$; $p = 0.032$). Ephemeroptera abundance was also associated with pH (Figure 1.2b; $R^2 = 73.8\%$; $t_7 = 4.44$; $p = 0.003$). Diptera family richness was also depressed at the more acidified sites (Figure 1.3; $R^2 = 77.9\%$; $t_7 = 4.96$; $p = 0.002$), but this relationship was not significant when the most acidic site (an influential point) was removed from the analysis. Diptera abundance was not associated with pH ($t_7 = -0.75$; $p = 0.480$). Stream pH was not a significant predictor of Trichoptera family richness ($t_7 = 1.16$; $p = 0.286$) or abundance ($t_7 = 0.61$; $p = 0.559$).

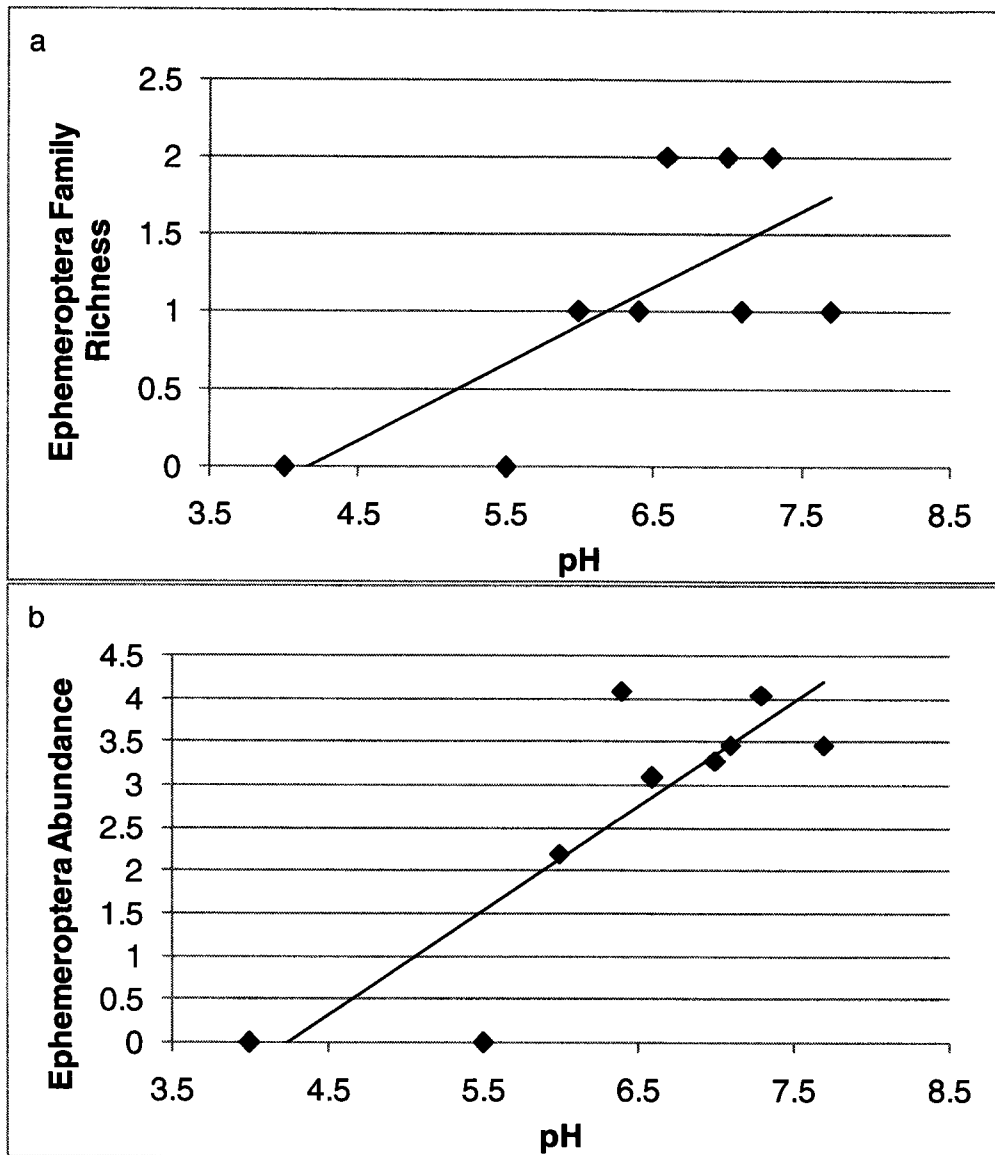


Figure 1.2. Association of pH and Ephemeroptera family richness (a) and log-transformed Ephemeroptera abundance expressed as $\ln(1+\text{number of individuals})$ where the number of individuals was pooled from among the nine kicknet samples collected at each site (b)

Plecoptera were found in greatest numbers at the most acidified sites (Figure 1.4; $R^2 = 49.4\%$; $t_7 = -2.61$; $p = 0.035$), though this relationship was not significant when the most acidic site (an influential point) was removed from the analysis. An increased abundance of leuctrid stoneflies at acidic sites was responsible for the increase in

Plecopteran invertebrates at acidified sites (Figure 1.5; $R^2 = 48.7\%$; $t_7 = -2.58$; $p = 0.037$).

Larger numbers of nemourid stoneflies were also found at acidic sites, but this trend was not quite statistically significant ($t_7 = -2.28$; $p = 0.057$).

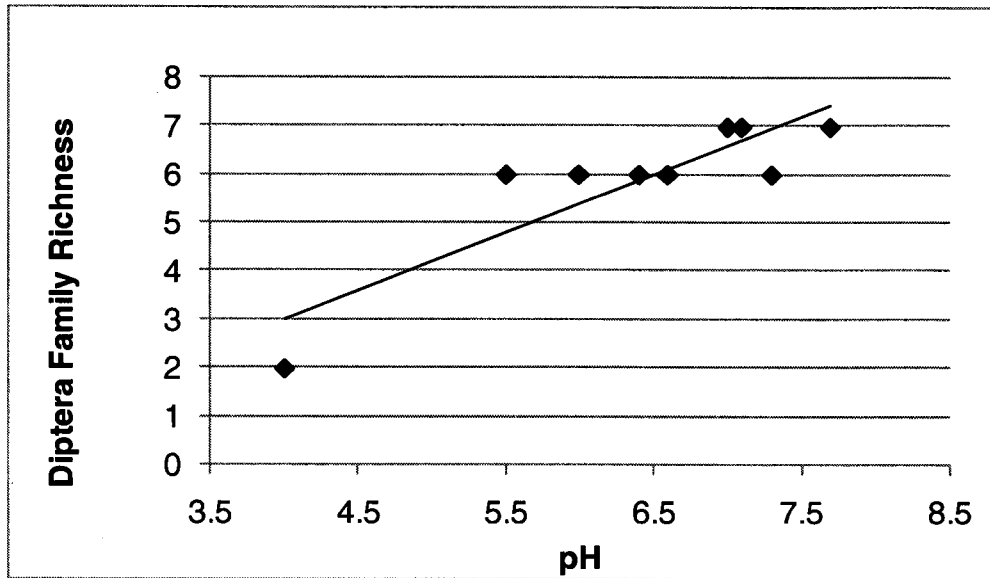


Figure 1.3. Relationship between pH and Diptera family richness

As shown in Figure 1.6, GPP ($t_7 = -1.16$; $p = 0.283$), R ($t_7 = 0.83$; $p = 0.434$), and P/R ($t_7 = -0.85$; $p = 0.425$) were not significantly associated with pH. GPP was significantly predicted by ammonium concentration ($R^2 = 79.2\%$; $t_7 = 5.16$; $p = 0.001$; Figure 1.7a). Higher rates of GPP were also significantly associated with lower concentrations of nitrate ($R^2 = 46.1\%$; $t_7 = -2.45$; $p = 0.044$; Figure 1.7b), but this relationship was not significant when the site with the lowest nitrate concentration (LKV, an influential point) was removed from the analysis.

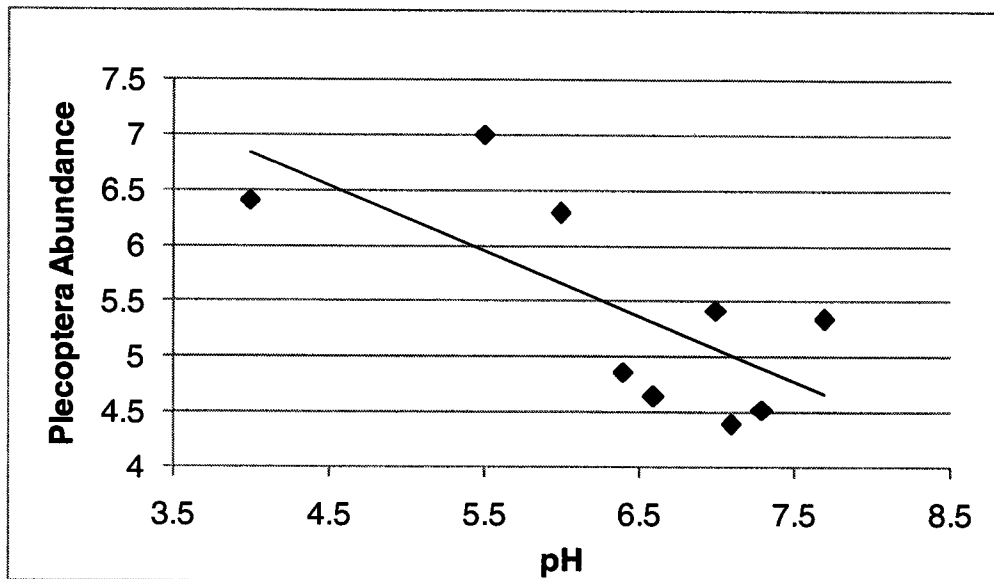


Figure 1.4. Association of pH and log-transformed Plecoptera abundance expressed as $\ln(1+\text{number of individuals})$ where the number of individuals was pooled from among the nine kicknet samples collected at each site

Isotopic signatures of macroinvertebrate food sources were not significantly associated with pH (Pillai's Trace = 0.0495; $F_{2,55} = 1.43$; $p = 0.248$). All multivariate contrasts among isotopic signatures of the five food sources were significant at the 95% confidence level except for those between periphyton and FPOM, bryophytes and leaves, and CPOM and leaves (Table 1.2). Macroinvertebrate isotopic signatures were not significantly associated with habitat (Pillai's Trace = 0.0109; $F_{4,146} = 0.20$; $p = 0.9377$); however, pH (Pillai's Trace = 0.212; $F_{2,72} = 9.69$; $p = 0.0002$) and family membership (Pillai's Trace = 0.447; $F_{4,146} = 10.51$; $p < 0.0001$) were both significant predictors of macroinvertebrate isotope values. An interaction term between pH and family membership was not a significant predictor of macroinvertebrate isotopic signatures (Pillai's Trace = 0.0276; $F_{4,146} = 0.51$; $p = 0.7278$).

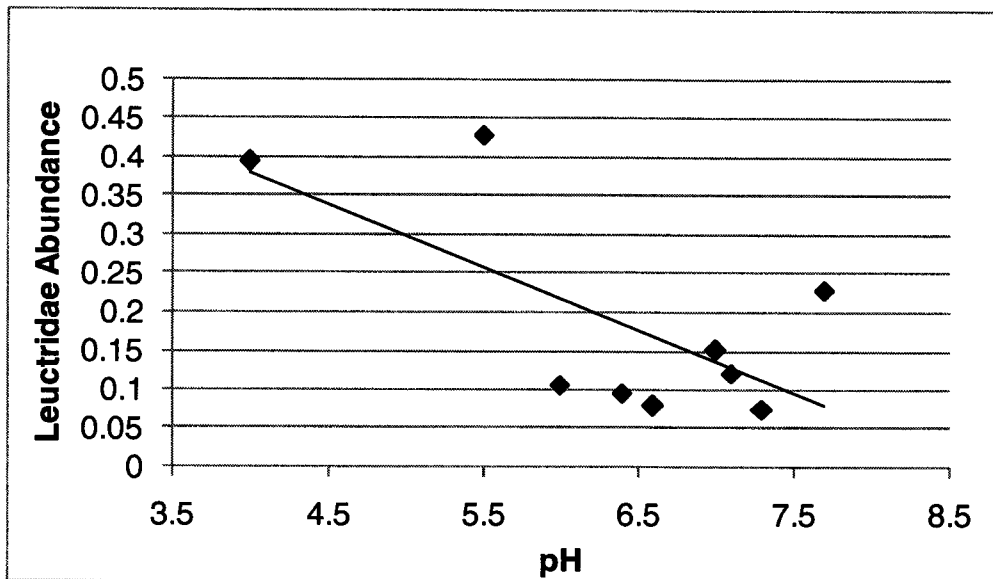


Figure 1.5. Association of pH and log-transformed Leuctridae abundance expressed as $\ln(1+\text{number of individuals})$ where the number of individuals was pooled from among the nine kicknet samples collected at each site

Although centroids of three primary food sources (periphyton, CPOM, and bryophytes) were distinct, the majority of measured and modeled isotopic signatures for macroinvertebrates collected from the least and most acidified stream sites fell outside of this range, assuming a trophic fractionation of 3.4‰ in ^{15}N during assimilation of food sources by macroinvertebrates (Minagawa and Wada 1984). Thus, it was not possible to use mixing-models to quantify the change in contribution of these three food sources to macroinvertebrate diet along the acidification gradient. However, while analyzed samples apparently do not encompass the full isotopic variability of macroinvertebrate food sources, the shift in macroinvertebrate isotope signatures with pH suggests that the diets of all three macroinvertebrate families include less periphyton and more allochthonous sources at acidified sites (Figure 1.8).

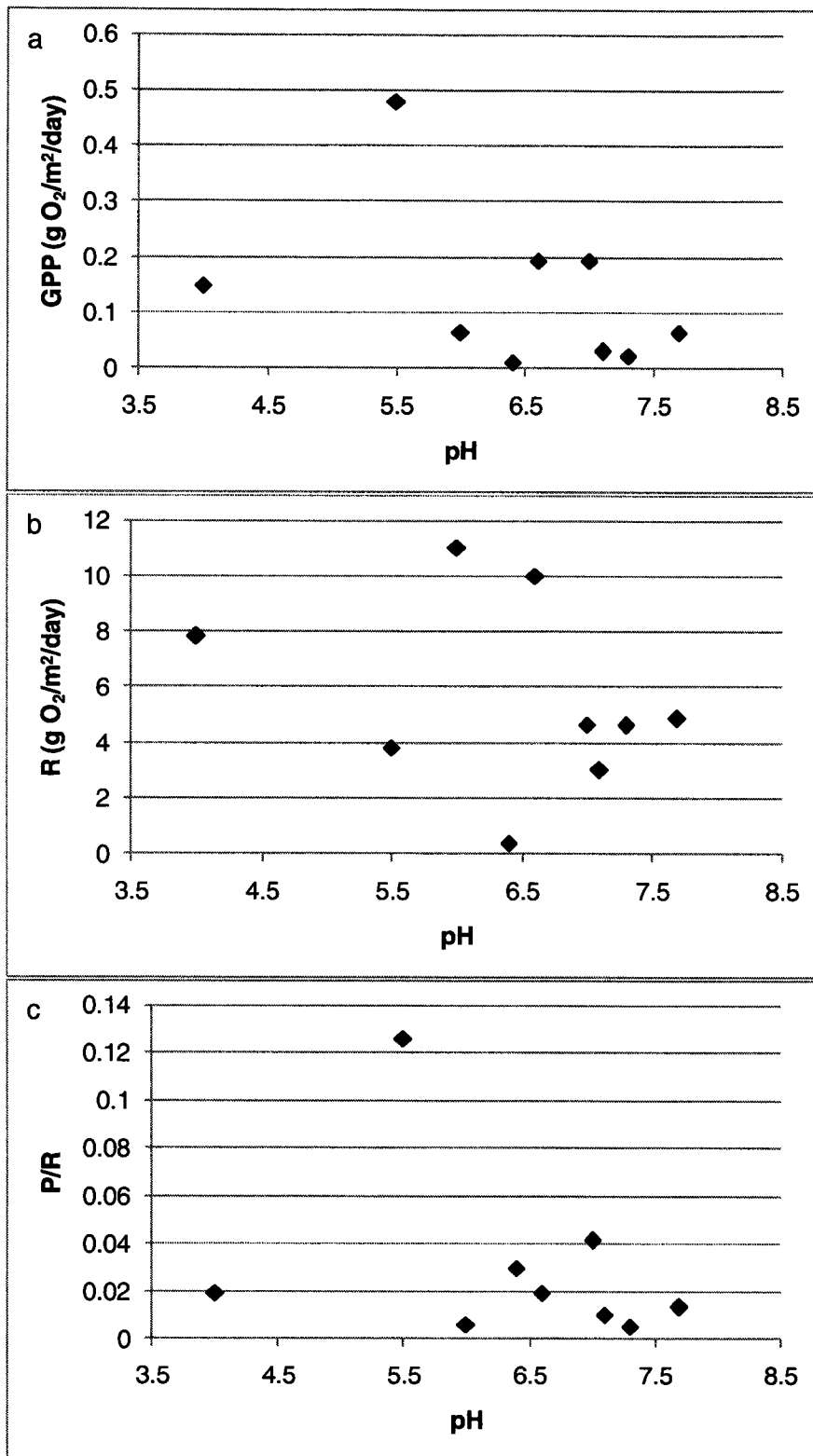


Figure 1.6. Relationships between GPP (a), R (b), and P/R (c) and pH

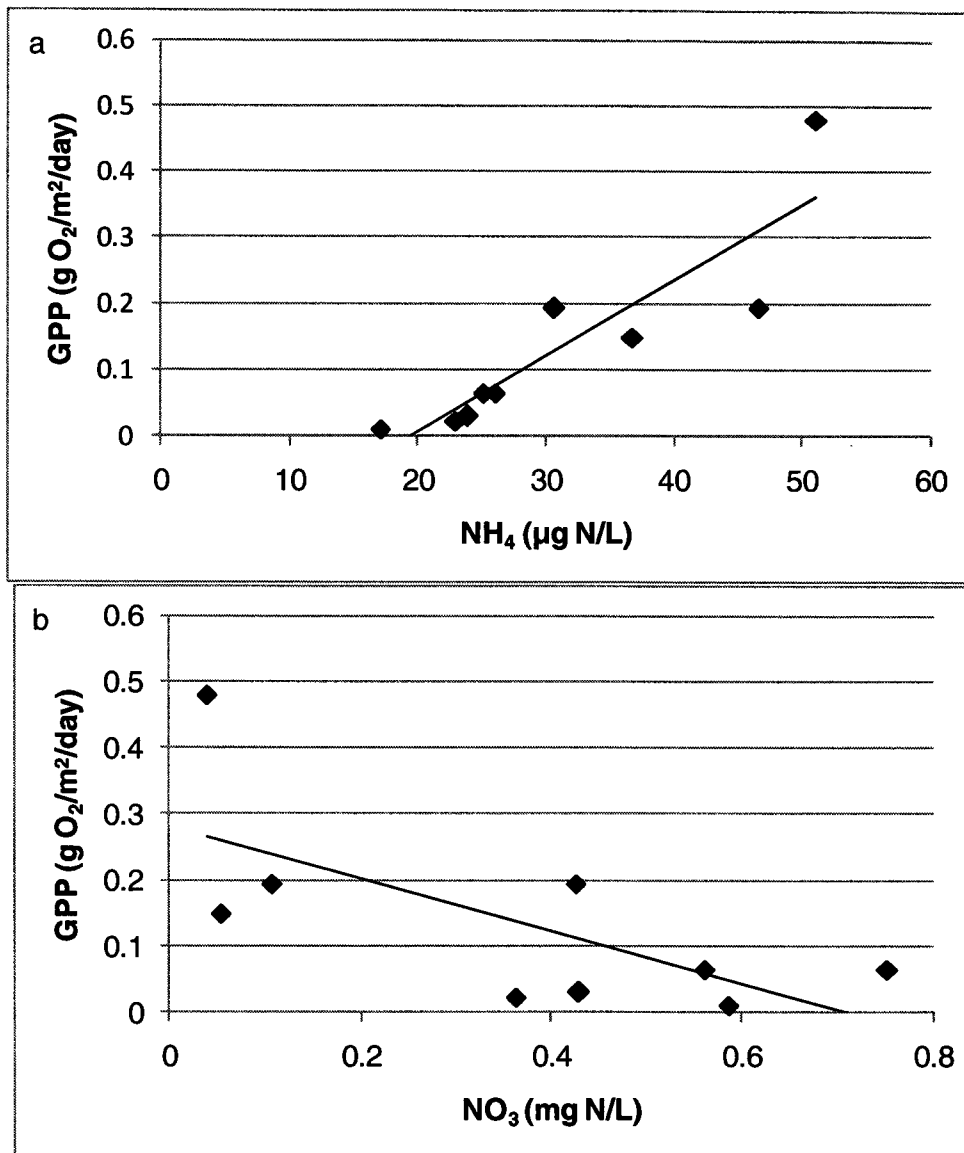


Figure 1.7. Relationships between GPP and ammonium (a) and nitrate (b)

Table 1.2. Results of multivariate contrasts among macroinvertebrate food sources isotopic signatures

First Food Source	Second Food Source	Pillai's Trace	F _{2,56}	p
Periphyton	Bryophytes	0.350	15.07	<0.0001
Periphyton	CPOM	0.203	7.14	0.0017
Periphyton	FPOM	0.0838	2.56	0.0861
Periphyton	Leaves	0.371	16.54	<0.0001
Bryophytes	CPOM	0.168	5.65	0.0058
Bryophytes	FPOM	0.377	16.97	<0.0001
Bryophytes	Leaves	0.0804	2.45	0.0956
CPOM	FPOM	0.332	13.91	<0.0001
CPOM	Leaves	0.0809	2.47	0.0941
FPOM	Leaves	0.451	23.05	<0.0001

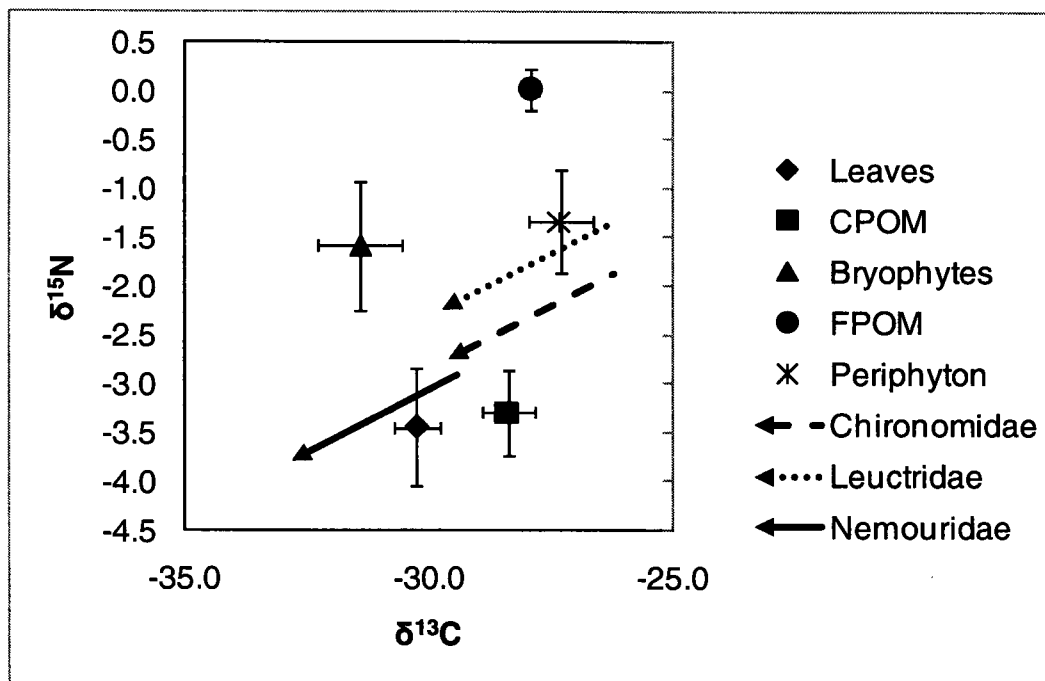


Figure 1.8. Stable isotope composition of macroinvertebrate food sources and shifts in macroinvertebrate isotopic signatures. Error bars show +/- 1 standard error around mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of food sources. Vectors indicate magnitude and direction of modeled change in isotopic signatures of macroinvertebrate families with the decline in stream pH from 7.7 to 4.0 (vector $\delta^{15}\text{N}$ values are reduced by 3.4 ‰ to account for trophic enrichment in order to better correspond with potential food sources).

Discussion

Our results documenting a reduction in macroinvertebrate family richness associated with low pH are consistent with a large body of research on this topic (Schindler 1988). Although overall macroinvertebrate abundance was not associated with pH, changes in community composition were evident, with the reduced abundance of Ephemeroptera at the most acidified sites offset by greater numbers of Plecoptera. The increased abundance of the families Leuctridae and Nemouridae at the most acidified sites is also consistent with past studies that have documented the domination of acid streams throughout the eastern United States, Canada, and Great Britain by the same families (Griffith and Perry 1993). Groom and Hildrew (1989) suggested that nemourid and other shredding invertebrates may be favored in acidified streams due to the abundance of coarse detritus that, despite its poor quality, is available throughout the year as a result of slow microbial decomposition. Hall et al. (1987) provided an evolutionary and physiological explanation for the changes in community composition and reduced biodiversity of macroinvertebrates in acid streams; they suggested that macroinvertebrates most sensitive to acidification (particularly mayflies) tend to belong to taxonomic groups that have spent the greatest amount of evolutionary time in aquatic environments, and these groups are most challenged in regulating their internal ion balance at low stream pH due to the large portion of their body surface area used for cutaneous respiration and ion regulation.

The effect of acidification on whole-stream metabolism is poorly documented in the literature. Whole-stream metabolism was not significantly associated with acidity in the nine stream sites examined for this study. It is important to note that nine sites is a

small sample size and that an underlying trend could potentially become apparent with a greater number of data points. The results of this study, however, suggest that ammonium concentration plays a greater role in regulating GPP than does pH in small streams in the Czech Republic. This result is consistent with several other studies that have found GPP to be closely associated with nutrient concentration (Mulholland et al. 2001, Bott et al. 2006).

This study provides an opportunity to compare the relative sensitivity of a structural metric (macroinvertebrate diversity) with that of a functional metric (whole-stream metabolism) to determine which acts as a better indicator of acidification. Schindler (1987) proposed that functional metrics would be less sensitive to ecosystem disturbance than would structural metrics, suggesting that ecosystem functions are buffered by feedback mechanisms. However, Gessner and Chauvet (2002) suggested that concerns regarding these types of compensatory responses were based more on intuition rather than on the results of empirical studies, and several subsequent studies demonstrated circumstances in which functional measures were better indicators of anthropogenic disturbance to aquatic systems. Bunn and Davies (2000) found that whole stream metabolism was a more sensitive indicator of nitrogen pollution than was community structure, and Schultheis et al. (1997) found that leaf decomposition rates were more sensitive to copper pollution than were community metrics. Recently, Young et al. (2008) advocated for the use of leaf breakdown and ecosystem metabolism as indicators of stream health in addition to structural metrics. More research is needed to better identify circumstances in which functional indicators are likely to improve the ability to detect ecosystem disturbance in aquatic systems. Our results suggest that

whole-stream metabolism is not as sensitive to acidification in small streams as are macroinvertebrate community metrics.

Our results support the idea that periphyton is an important food source even in small headwater streams, which are dominated by detritus (Peterson et al. 1993a, Finlay 2001). Our data also support the hypothesis that loss of herbivory in acidified streams does not result solely from reductions in scraper/grazer macroinvertebrates. The shifts I documented in isotopic signatures of Chironomidae, Leuctridae, and Nemouridae in acidified streams may result from species-level dietary changes. Alternatively, these isotopic shifts may reflect replacement of species within these three families by species that rely more heavily on detritus, possibly due to establishment of less palatable periphyton (Junger and Planas 1993). If acidification results in the replacement of specialist macroinvertebrate feeders by generalist species, reinvasion by extirpated species upon recovery of stream chemistry may be competitively excluded (Ledger and Hildrew 2005, Monteith et al. 2005).

In conclusion, acidification is a persistent problem for small Central European streams. Significant and predictable reductions in macroinvertebrate diversity were associated with stream pH. Although I found a clear association of acidification with changes in food-web dynamics, further study is needed to determine whether family-level shifts in isotopic signatures result from species-level dietary changes or species replacement at low pH sites. Whole stream metabolism does not appear to be as sensitive an indicator of acidification as are macroinvertebrate metrics. However, whole-stream metabolism measurements in a larger number of acidified streams would be helpful in establishing more definitively whether this ecosystem function is influenced by pH.

CHAPTER 2

STREAM ECOSYSTEM RESPONSE TO AN EXTRAORDINARY FLOOD EVENT: A WINDOW INTO THE FUTURE OF TEMPERATE STREAMS?

Abstract

The Suncook River in Epsom, New Hampshire dramatically changed course on May 15, 2006 after 20 cm of rain fell over a two-day period. This avulsion created one entirely new stream reach, dewatered a second reach, and delivered large amounts of sediments to an otherwise un-impacted downstream reach. While dramatically high levels of suspended sediment concentrations in and downstream of the new channel recovered to background levels within approximately two months, reduced substrate particle size in these areas were associated with reduced macroinvertebrate abundance, altered macroinvertebrate and fish communities, and reduced whole-stream respiration that persisted throughout the study period. Dewatering led to long-term changes in water chemistry, as well as changes to the fish community and reduced whole-stream respiration. Understanding geomorphic conditions that precede avulsions as well as ecosystem effects that result may become important for managing water resources under changing climate conditions that favor increased avulsion frequency.

Introduction

The natural process by which all or part of the flow of a river carves out a new channel and dewater a portion of the original river channel is termed an avulsion. For the few modern rivers for which such data exist, avulsion recurrence intervals vary widely from as short as 28 years for the Kosi River in India, to as long as 1400 years for the Mississippi River (Stouthamer and Berendsen 2001). While the specific geomorphic conditions necessary for initiating an avulsion cannot yet be defined (Slingerland and Smith 2004), there is reason to suspect that climate change may lead to increased avulsion frequencies; high rates of sedimentation (which occur during periods of sea-level rise) and frequently recurring floods of high magnitude have both been proposed as factors promoting avulsions (Slingerland and Smith 2004). Thus, understanding how stream ecosystems respond to avulsions may become increasingly important in achieving future stream management goals.

Documentation of the effects of avulsions on in-stream ecology is extremely rare, and the influence of avulsions on stream ecosystems is almost certainly underappreciated. In an investigation into the potential causes of recruitment failure of white sturgeon in the Canadian Nechako River, McAdam et al. (2005) found that a 1961 avulsion led to a “sediment wave” that altered stream bed substrates in white sturgeon habitat, in turn resulting in recruitment failure of the white sturgeon beginning in 1964 and continuing for over 40 years. In Mississippi, channel avulsion may also have contributed to upstream erosion (headcutting) many kilometers away in the Bayou Pierre system, resulting in the upstream migration of riffle habitats and associated riffle-inhabiting fish species (Ross et al. 2001). While research documenting the multiple effects of avulsions on stream

ecosystems is virtually nonexistent, the predicted effects of avulsions can be broken down in terms of those due to dewatering, new channel development, and sedimentation (downstream of the newly eroding channel), all of which have received considerably more attention.

Dewatering

A channel abandoned due to an avulsion may retain some flow if the avulsion was not complete, or if flow is contributed by one or more tributaries to the abandoned channel. The direct and indirect impacts of partial dewatering of a stream can greatly reduce population densities and species richness as well as alter life-history schedules, species composition, patterns of abundance, type and strength of biotic interactions (predation and competition), food resources, trophic structure and ecosystem processes (Lake 2003). Dewatering results in a reduction of habitat space in streams, as well as increased longitudinal fragmentation of habitat, as shallow riffle and run sections of the stream dry up and distinct pools remain (Lake 2000). Organic matter and sediments accumulate in these pools, which in turn can lead to a decrease in DO concentrations and an increase in nutrient concentrations (Stanley et al. 1997, Acuna et al. 2005).

Reduction of habitat and increased longitudinal fragmentation has been shown to leave organisms such as prosobranch snails and cased caddis larvae stranded on exposed areas of the riverbed (Extence 1981). McIntosh et al. (2002) documented a 46% reduction in macroinvertebrate density below a diversion in Iao Stream, Maui, Hawaii. In turn, reduced macroinvertebrate production during drought conditions in West Virginia led to a reduction in brook trout populations in forested headwater streams (Hakala and

Hartman 2004). Other impacts of dewatering on stream biota include extremely low community abundance, *Gammarus pulex* abundance and the Berger-Parker dominance index, and extremely high values of the Shannon Wiener and Simpson diversity indices in a groundwater dominated river (Wood and Armitage 2004).

New channel development

New river channels formed by avulsions provide an opportunity to study primary succession, defined by Fisher (1990) as involving “site-specific, temporal change occurring after a disturbance that is so intense that no trace of the previous community remains.” Primary succession has rarely been documented in streams at the spatial scale of whole river segments (Milner 1994). Studies investigating colonization of small natural and artificial substrates by benthic macroinvertebrates have documented site-specific succession at small scales in streams (Lake and Doeg 1985, Downes and Lake 1991). Dispersal mechanisms assumed to explain observed colonization patterns include upstream migration, downstream drift, lateral and vertical migration from the hyporheic zone, and aerial oviposition (Malmqvist et al. 1991). Investigations of reach-scale benthic macroinvertebrate colonization have been carried out on new man-made channels (Gore 1982, Malmqvist et al. 1991), streams rewatered after severe drought (Hynes 1975), and a new stream formed following glacial recession in Alaska (Milner 1994). Global comparisons of early colonizers of experimental patches, disturbed reaches, newly watered channels, and disturbed rivers reveal concordance at the family and generic levels (Mackay 1992), though mechanisms governing the interaction among benthic macroinvertebrate species in early successional streams are still far from explained

(Malmqvist et al. 1991). Furthermore, while these studies do offer insight into the course of benthic macroinvertebrate colonization in lotic systems, even fewer provide information regarding other aspects of ecosystem structure and function in newly formed river reaches.

Sedimentation

As a new channel is carved out of a river's floodplain following an avulsion, eroded sediment will be deposited in and downstream of this new channel. Sedimentation of streams affects organisms in two major ways: through physical and chemical changes to the water, and through blanketing of the stream bottom. Specific effects of siltation on aquatic systems include screening out light, changing heat radiation, smothering the stream bottom, and retaining organic material and other substances, which create unfavorable conditions at the bottom (Ellis 1936). By reducing the stream bottom's permeability to water movement, an increased amount of fine sediments in the streambed can affect the delivery and removal of gases, nutrients and metabolites, and potentially movement of animals (Allan 1995). Suren et al. (2005) suggested that sublethal effects of sedimentation including behavioral avoidance and changes in habitat and food conditions may explain the disappearance of sensitive invertebrates from catchments that are subject to frequent episodes of high suspended sediment. This type of behavioral avoidance was demonstrated by Rosenberg and Wiens (1978), who found that experimentally increasing suspended sediment in a northern Canadian river significantly increased macroinvertebrate drift rates. Wood et al. (2005) found that the response of individual macroinvertebrate taxa to burial with sediments in ex-situ experiments was highly

variable. They suggested that many of the documented changes to benthic macroinvertebrate community composition due to sedimentation probably mask a variety of individual faunal responses.

These changes in macroinvertebrate community composition have been described in several studies. Thompson et al. (2005) found macroinvertebrate density, algal biomass, and diatom species richness declined significantly downstream of a Pennsylvania dam following complete dam removal and transport of sediments downstream, but overall assemblage structure downstream remained similar to upstream control sites throughout the study for both invertebrates and diatoms. Rabeni et al. (2005) found that densities of all the feeding groups decreased significantly along continuums of deposited sediments in reaches where other habitat characteristics were similar. They noted a significant increase in relative densities of gatherers, and a significant decrease in taxa richness for all the feeding groups except for the shredders. In a Canadian forest headwater stream manipulated to induce fine sediment inputs, only small reductions in diversity and richness of spring communities were noted. These reductions resulted from a significant decline in the proportion of spring shredders, accompanied by a significant increase in the percent Chironomidae (Kreutzweiser et al. 2005).

Changes in fish communities due to sedimentation have been documented in several studies. Natsumeda (2003) found that a severe flood on the Inabe River in central Japan had a negative impact on refuge abundance (due to sedimentation), condition factor (as determined by fish weight and standard length), and population density of Japanese fluvial sculpin. The increased turbidity and reduction of instream habitat diversity related to sedimentation in a South American stream affected by gold mining led to changes in

fish community structure including low species diversity and low proportion of young fishes (Mol and Ouboter 2004). In the Etowah River in the southeastern U.S., high baseflow turbidity and fine stream beds were associated with homogenized fish assemblages as defined by lower ratios of endemic to cosmopolitan species richness (Walters et al. 2003). Changes in relative abundance of fishes requiring different spawning habitats were noted in small streams in the upper Little Tennessee River basin of North Carolina (Sutherland et al. 2002); fish requiring clean gravel or cobble for spawning were found in less disturbed watersheds with lower suspended and bedload sediment transport, while mound-building fish such as cyprinids were found in streams with higher rates of sedimentation.

There is also evidence that sedimentation can lead to changes in stream metabolism. Davies-Colley et al. (1992) found that suspensions of clays seeping into the streams due to placer gold-mining on the West Coast of the South Island of New Zealand resulted in a reduction of light and a proportional reduction in benthic primary productivity. In turn, benthic algal biomass and phototrophic content of the epilithon were reduced. Yamada and Nakamura (2002) also found that the accumulation of fine sediment reduced light penetration for photosynthesis, resulting in lowered periphyton levels in a river in northern Japan. Rier and King (1996) noted changes in community metabolism and periphyton biomass due to unstable sand substrates brought on by channelization. They found that respiration and photosynthesis were severely depressed, resulting from low periphyton biomass in sandy sections of an agriculturally disturbed stream. In this case, periphyton colonization may have been limited due to the abrasive substrate, rather than reduced light penetration. Wood and Armitage (1997) reviewed

studies documenting the causes and extent of sedimentation in the lotic environment and its impact on stream ecology.

Case Study

On May 15, 2006, a large flood triggered an avulsion on the Suncook River in New Hampshire, naturally creating a new stream reach of approximately 800 m. This new reach flows through a wetland along the edge of an old railroad bed before converging on an access road, flowing into a sand pit, and rejoining the original river channel. Erosion of this new channel has led to severe downstream sedimentation. Creation of the new stream reach also resulted in nearly complete dewatering of the 2.5 km abandoned channel, which is now fed only by Mason Brook, a small tributary.

I have used this opportunity to study the impact of the Suncook River avulsion on in-stream physical, biological, and biogeochemical parameters in the affected reaches. I sought to document the rate of recovery following the initial avulsion disturbance, as well as long-term changes in biological communities and ecosystem function resulting from physical changes in the affected reaches of the Suncook River system. I hypothesized that fish and macroinvertebrate communities would be altered by sedimentation and dewatering. I further hypothesized that whole-stream metabolism would be depressed in and downstream of the newly formed Suncook River channel, where high rates of erosion and sedimentation have resulted in unstable stream bed substrates and high levels of suspended sediment.

Methods

Study Site

The fourth-order Suncook River, a tributary of the Merrimack River, is located in southeastern New Hampshire. It drains a watershed of approximately 575 km² and has an average annual discharge of approximately 9 m³ s⁻¹. The May 15, 2006 avulsion occurred during a large flood following a rain event during which over 20 cm of rain fell during a two-day period. I established sampling sites in the Suncook River system in the newly formed channel, the dewatered channel, the heavily sedimented channel downstream of the avulsion, and at an upstream reference site, as well as at the outlet of Mason Brook (Figure 1).

Sampling

Streamwater chemistry samples were collected from all Suncook River sites as well as at the outlet of Mason Brook every two weeks beginning approximately two weeks after the avulsion and continuing for approximately 14 months (Figure 2.1). Samples were filtered in the field using pre-combusted glass fiber filters (0.7 µm pore size), and frozen until analysis. All samples were analyzed in the Water Quality Analysis Lab of the Water Resources Research Center on the campus of the University of New Hampshire, Durham, NH. Methods for analyses include ion chromatography (NO₃⁻, Na⁺, K⁺, Ca²⁺, Mg²⁺, Cl⁻, SO₄²⁻), discrete colorimetric analysis (NH₄, PO₄, NO₃/NO₂), and high temperature oxidation (DOC, TDN).

Stratified Wolman (1954) pebble counts were carried out in all Suncook River sites twice (10/06 and 8/07) to characterize coarse surface substrate. Intermediate axes

were measured using a ruler and hand-held gravel analyzer (Gravelometer, US SAH-97, Wildlife Supply Company, Buffalo, NY) for at least 100 particles.

Three replicate benthic macroinvertebrate samples were collected from all Suncook River sites quarterly (7/06, 9/06, 2/07, 5/07, 8/07) using a drift net (28 cm tall by 47 cm wide with a mesh size of 500 μ m) and by scrubbing all rocks and disturbing sediment within 30 cm of the kicknet frame. On 2/07, only two replicate samples could be collected from the Dewatered site due to ice cover. Specimens were preserved in 70% ethanol and subsampled according to EPA's Rapid Bioassessment Protocol for benthic macroinvertebrate collection. Specimens were identified to the family level, except for Oligochaeta and Hirudinea (identified to class). Fish were surveyed at the Reference, New-Midstream, Sedimented, and Dewatered sites (Figure 2.1) once (8/07) with backpack electroshockers in collaboration with the New Hampshire Fish and Game Department.

Whole-stream metabolism was measured in the reference, dewatered, new channel, and sedimented channel reaches of the Suncook River system once (9-10/07) using a 1-station diurnal O₂ curve approach (Houser et al. 2005). Dissolved oxygen concentrations were logged at 5-minute intervals at the "Dewatered" sampling site and at the downstream ends of the reference reach, new channel, and sedimented reach (immediately upstream of the confluence with the dewatered west branch). Loggers were deployed simultaneously for 48 hours in the reference, new, and sedimented reaches, and then again simultaneously for 72 hours in the reference and dewatered reaches. Barometric pressure data in approximately 15-minute intervals were obtained from Concord Municipal Airport (located approximately 11 km from the study area) by way of

an online weather database (www.wunderground.com), which compiles information from airport weather stations throughout the country. Reaeration coefficients were calculated based on the semiempirical, energy-dissipation equation for low-flow, pool and riffle streams developed by Melching et al. (1999). Average wetted-width of the channel was measured at a minimum of three locations for each reach. Stream velocity and discharge

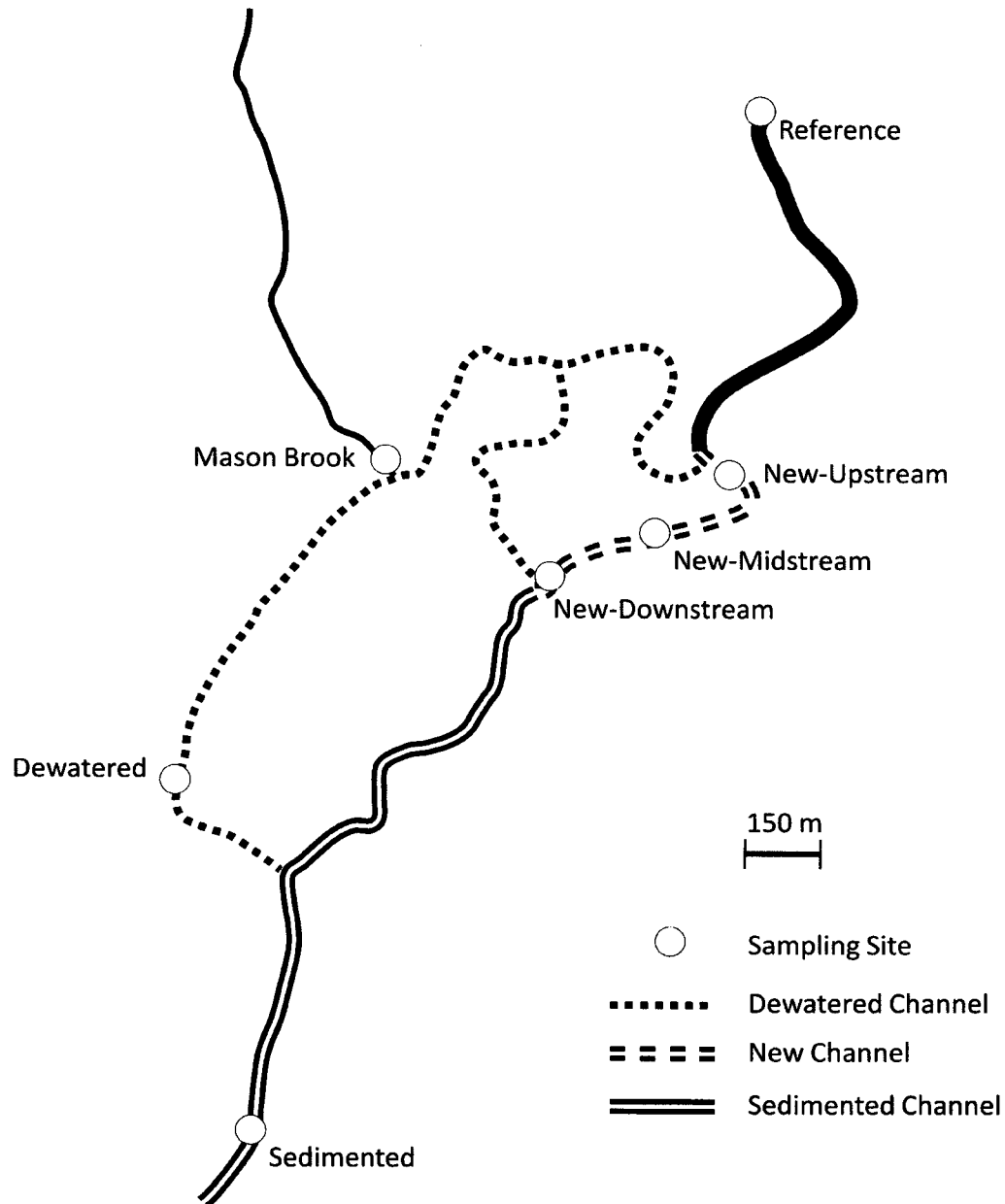


Figure 2.1. Suncook River system and sampling site locations

were determined in situ with a simultaneous slug injection of concentrated NaCl solution. Average water depth was computed as discharge divided by the product of average wetted width and average water velocity. Water-surface slope was determined using topographic maps. The change in dissolved oxygen concentration over 5-minute intervals was corrected for air-water O₂ exchange and then used to determine the net rate of dissolved oxygen change due to ecosystem metabolism over this interval. The rate of air-water O₂ exchange was calculated with the reaeration coefficient adjusted to the measured water temperature and estimated % dissolved oxygen saturation. Nighttime respiration (R) was calculated as the sum of net ecosystem metabolism occurring at night, and daytime R was interpolated between R rates measured 25 minutes before dawn and 25 minutes after dusk. Total daily R was calculated as the sum of nighttime and daytime R rates over 24 hours (midnight to midnight), and daily gross primary production (GPP) was calculated as the sum of the differences between interpolated daytime respiration rates and net ecosystem metabolism. P/R was calculated as the ratio of GPP to R.

Statistical Analysis

For each sampling date, one-way ANOVA using log-transformed data and Dunnett's comparisons was used to identify sites at which macroinvertebrate abundance was significantly different than the control reach at the 95% confidence level.

Best subsets regression was used to select the variables that were most important in controlling macroinvertebrate abundance (again log-transformed) at the six sampling sites over the course of this study. I included the following variables in this model: days since avulsion, median particle size, water velocity, specific conductance, suspended

solids, dissolved organic nitrogen, dissolved oxygen, and NO_3 (the last five parameters were averaged over the three water chemistry sampling dates prior to macroinvertebrate sampling).

Macroinvertebrate communities among the six macroinvertebrate sampling sites over the course of the study were compared using nonmetric multidimensional scaling (NMS) and multiresponse permutation procedures (MRPP). Taxa represented by fewer than three individuals were excluded from the analysis. Macroinvertebrate data were log-transformed for analysis as $\ln(1 + \text{number individuals})$. Before performing the ordination, the matrix was screened for outliers. Both NMS and MRPP were conducted using PC-ORD v. 4 (McCune and Mefford 1999) and the Sørensen (Bray-Curtis) distance measure. NMS was conducted using 40 runs of real data along with 50 runs of randomized data (a maximum of 400 iterations for each run) for a Monte Carlo test of significance that similar results could have been achieved by chance alone. Following Monte Carlo testing, a two-dimensional solution was chosen for the final iterative ordination using the best ending point in the preliminary analysis as the starting point in the final run. A secondary matrix of explanatory variables including month, median particle size, water velocity, specific conductance, suspended solids, dissolved organic nitrogen, dissolved organic carbon, dissolved oxygen, and NO_3 (the last six parameters expressed as averages over the three water chemistry sampling dates prior to macroinvertebrate sampling) was used to help interpret the ordination results.

Fish were divided into two age classes: young-of-year (YOY) and yearling or older using specific knowledge of species growth rates (Clugston and Cooper 1960) and by identifying histogram discontinuities in fish length data (J. Magee, personal

communication, September 17, 2010). To examine differences in fish communities among sample sites, fish data were analyzed both including and excluding YOY fish. Chi-square tests of independence were used to examine relationships between abundance of the five most common fish species and location, both including and excluding YOY fish. For each analysis, less abundant fish were grouped into an “other” category.

Whole-stream metabolism in the affected reach was compared with whole-stream metabolism in the reference reach using one-way ANOVA and Dunnett’s comparisons (New-Midstream and Sedimented sites) and two-sample t-tests (Dewatered site). P/R was log-transformed to equalize variance among groups.

Results

Geomorphology

Pebble count data are summarized in Figure 2.2. When quantified in October, 2006, median particle size steadily decreased from cobbles at the upstream reference and dewatered sites, to gravel in the new channel, to sand in heavily sedimented downstream portions of the Suncook River. Results of pebble counts carried out nearly 10 months later were nearly identical, demonstrating the persistence of this trend.

Water quality

As shown in Figure 2.3, exceptionally high concentrations of total suspended solids were documented in and downstream of the new channel during the month following the avulsion. While suspended sediment levels in and downstream of the new

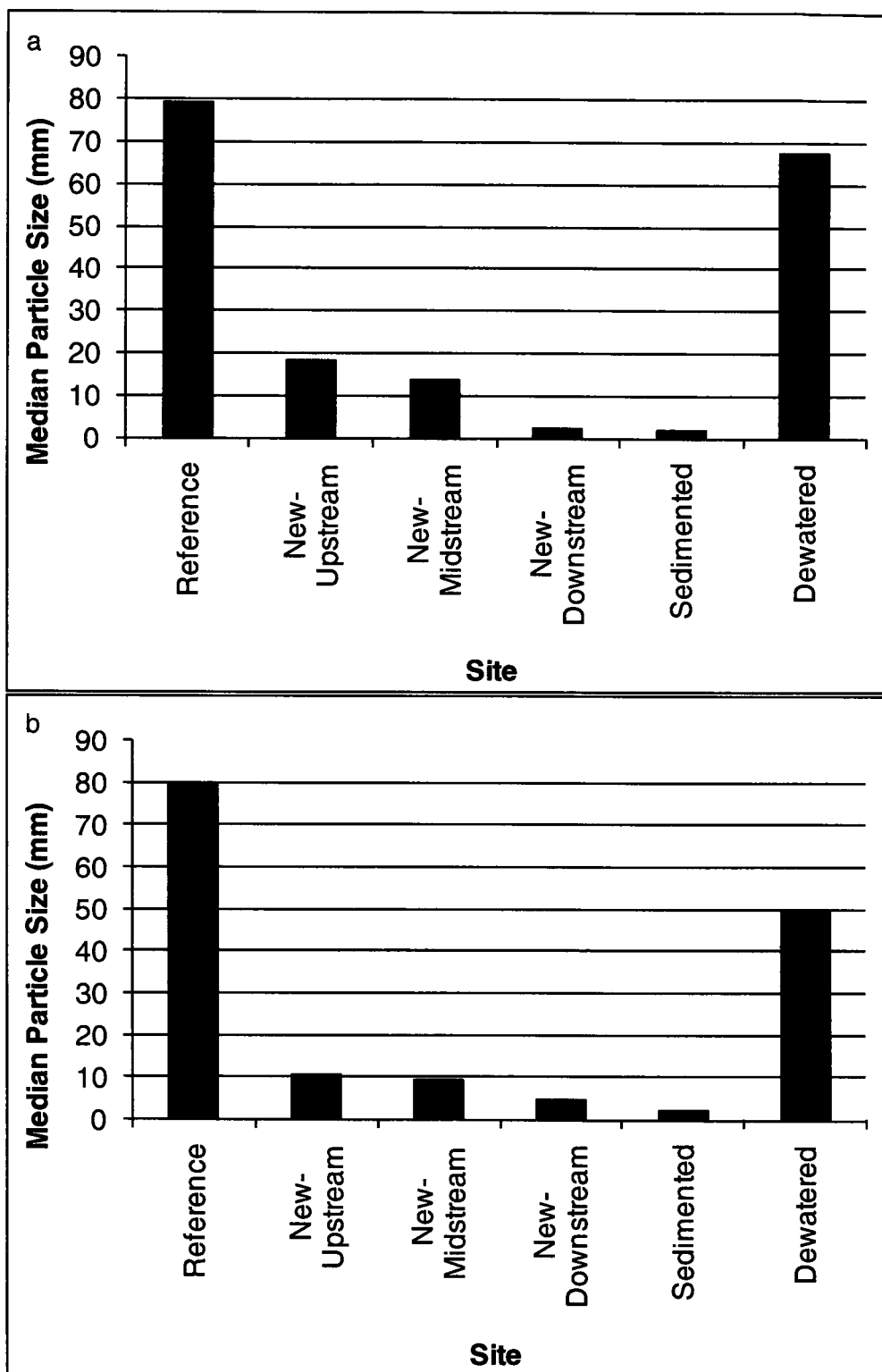


Figure 2.2. Median particle size in the Suncook River on 10/1/06 (a) and 8/15/07 (b)

channel declined over four months, suspended sediment concentrations at these sites in and downstream of the new channel remained higher and more variable than at the reference site for the extent of the study period.

The avulsion did not lead to major changes in water chemistry in the main channel of the Suncook River. However, dewatering of the west branch of the Suncook River did lead to long-term increases in the concentration of major ions (Figure 2.4a). Excepting nitrate, ion concentrations in the dewatered Suncook River channel following the avulsion closely matched ion concentrations documented in Mason Brook. On the other hand, nitrate concentrations in the dewatered reach were much higher than nitrate concentration in Mason Brook (Figure 2.4b). Concentrations of dissolved organic carbon

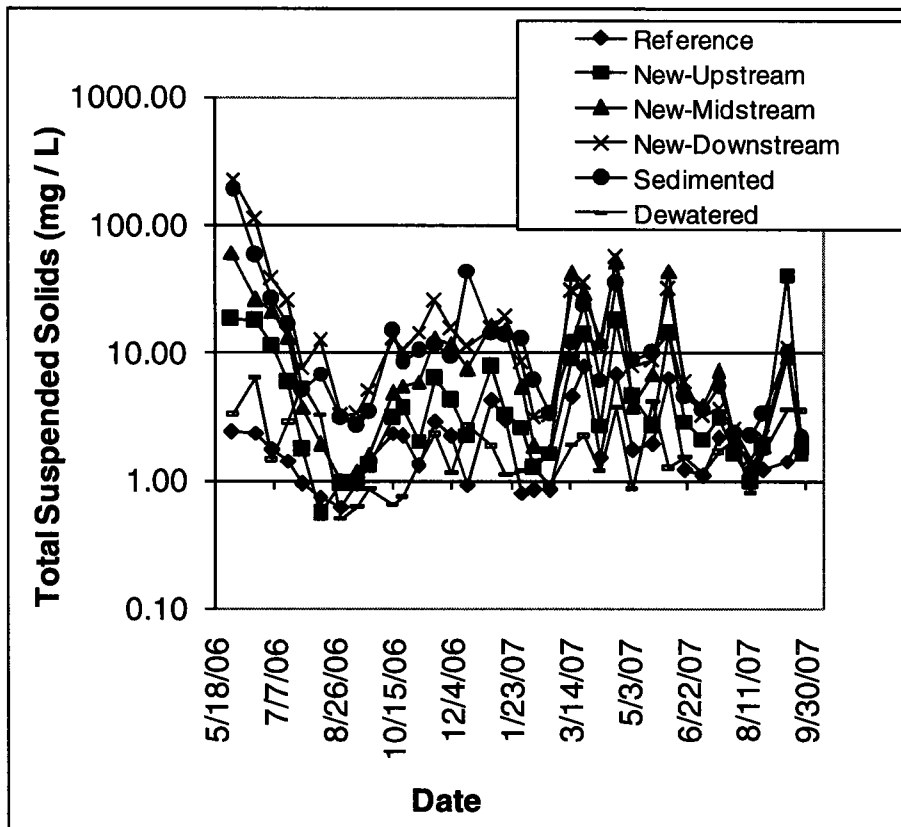


Figure 2.3. Total suspended solids at selected sites in the Suncook River during the 16 months following the May 2006 avulsion

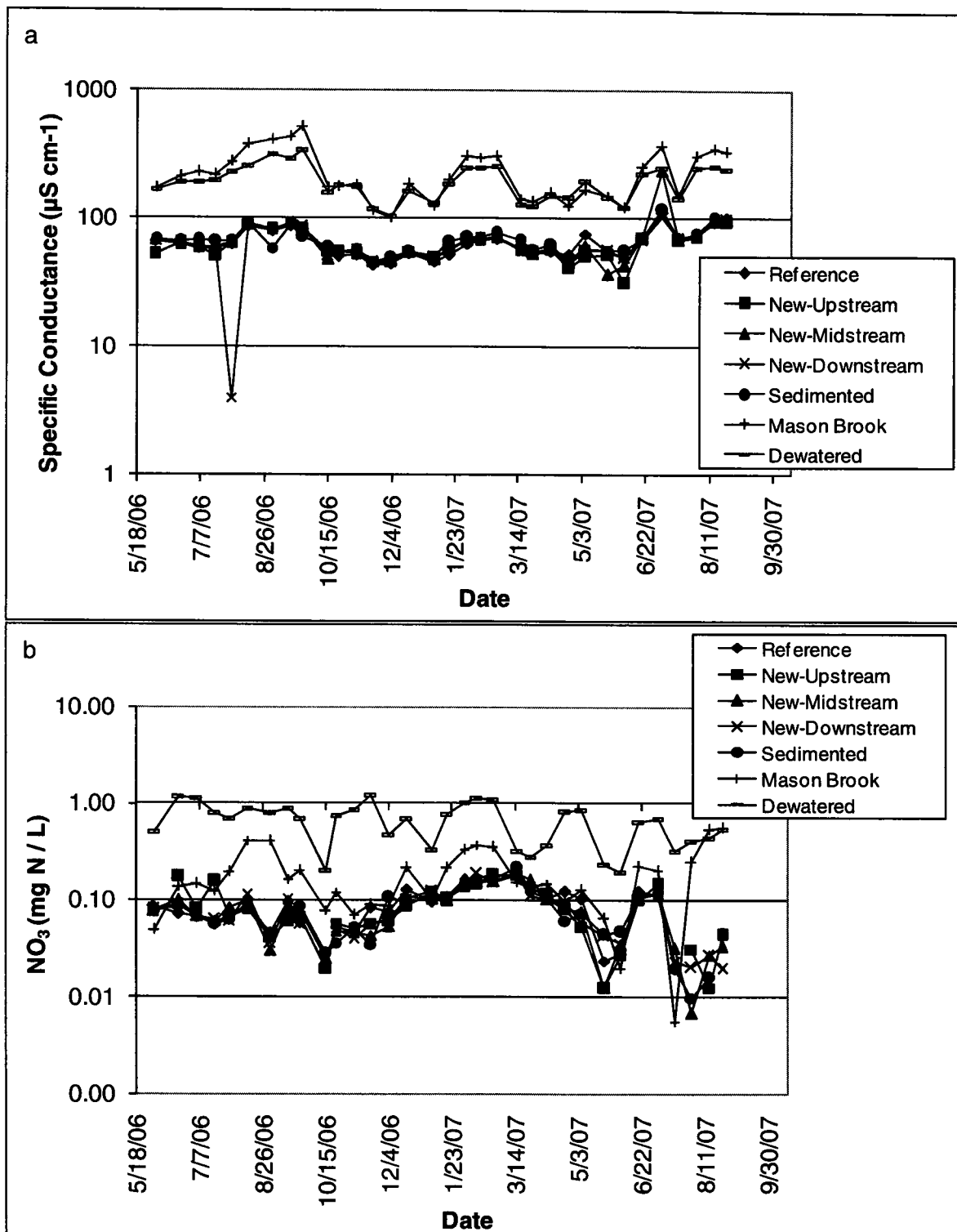


Figure 2.4. Specific conductance (a) and nitrate concentration (b) in the Suncook River and Mason Brook following the avulsion

in the dewatered channel and in Mason Brook were also slightly elevated as measured following the avulsion, but there were no noticeable differences in dissolved organic nitrogen among study sites (Figures 2.5a-b).

Biota

Following the avulsion and throughout the study period, macroinvertebrate abundance remained dramatically lower in and downstream of the new channel as compared with the reference and dewatered sites (Figure 2.6a-e). On all dates, macroinvertebrate abundance at the Sedimented and New Downstream sites was significantly lower than at the Reference site. Macroinvertebrate abundance at the New Midstream site was significantly lower than at the Reference site on two sampling dates (7/12/06 and 2/10/07). Macroinvertebrate abundance at the New Upstream and Dewatered sites was significantly lower than at the Reference site on 5/15/07 and 8/21/07, respectively.

A best subsets regression model was able to predict macroinvertebrate abundance with an adjusted R^2 of 56% using two variables, median particle size and suspended solids (Table 2.1). Greater macroinvertebrate abundance was associated with lower suspended sediment concentration at each site. Macroinvertebrate abundance was positively associated with median particle size.

NMS ordination indicated differences in macroinvertebrate communities among affected areas of the Suncook River system over the course of the study period. The two-axis NMS solution (stress = 12.6, instability = 0.031) represents 85.2% of the total

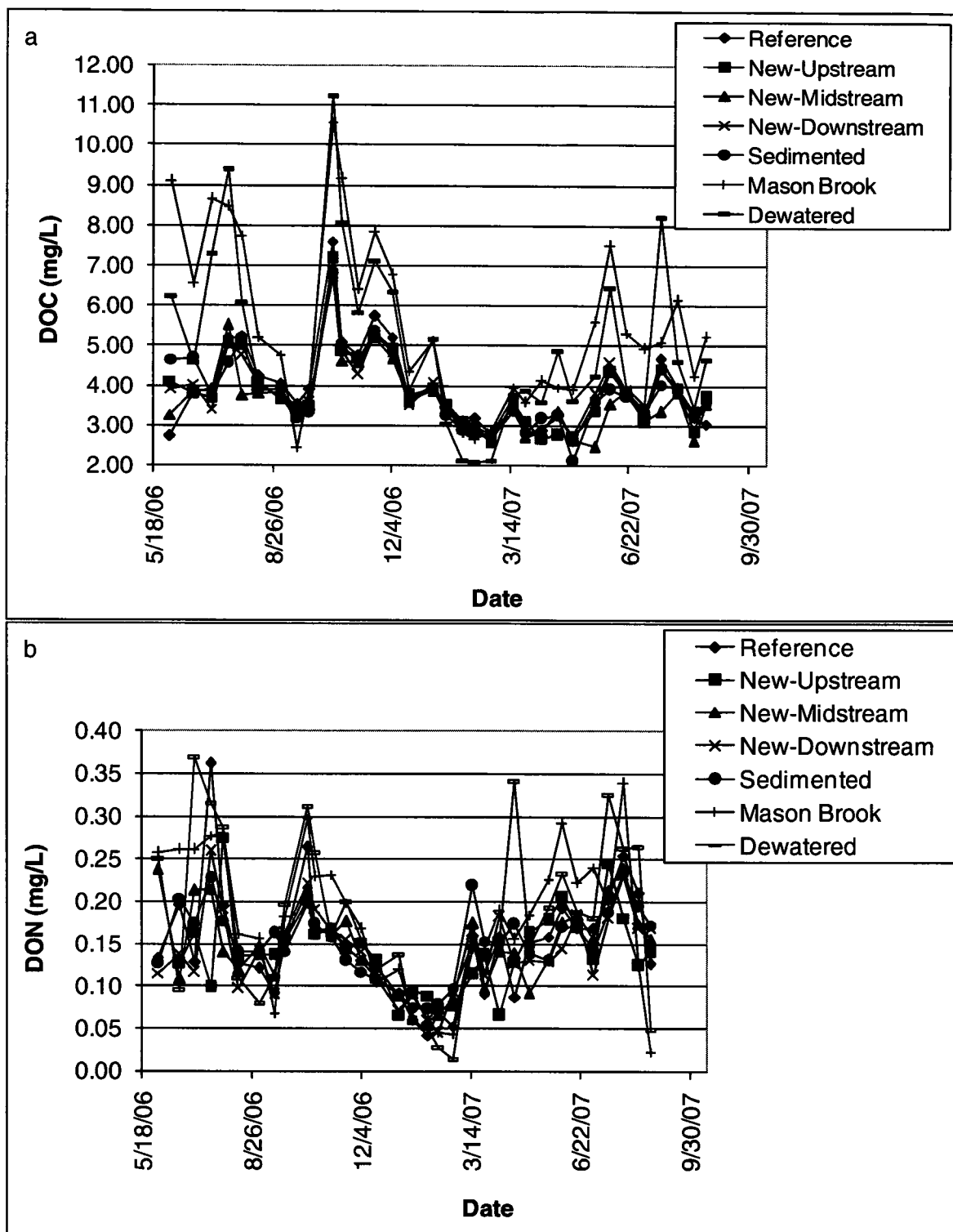


Figure 2.5. Dissolved organic carbon (a) and dissolved organic nitrogen (b) concentration in the Suncook River and Mason Brook following the avulsion

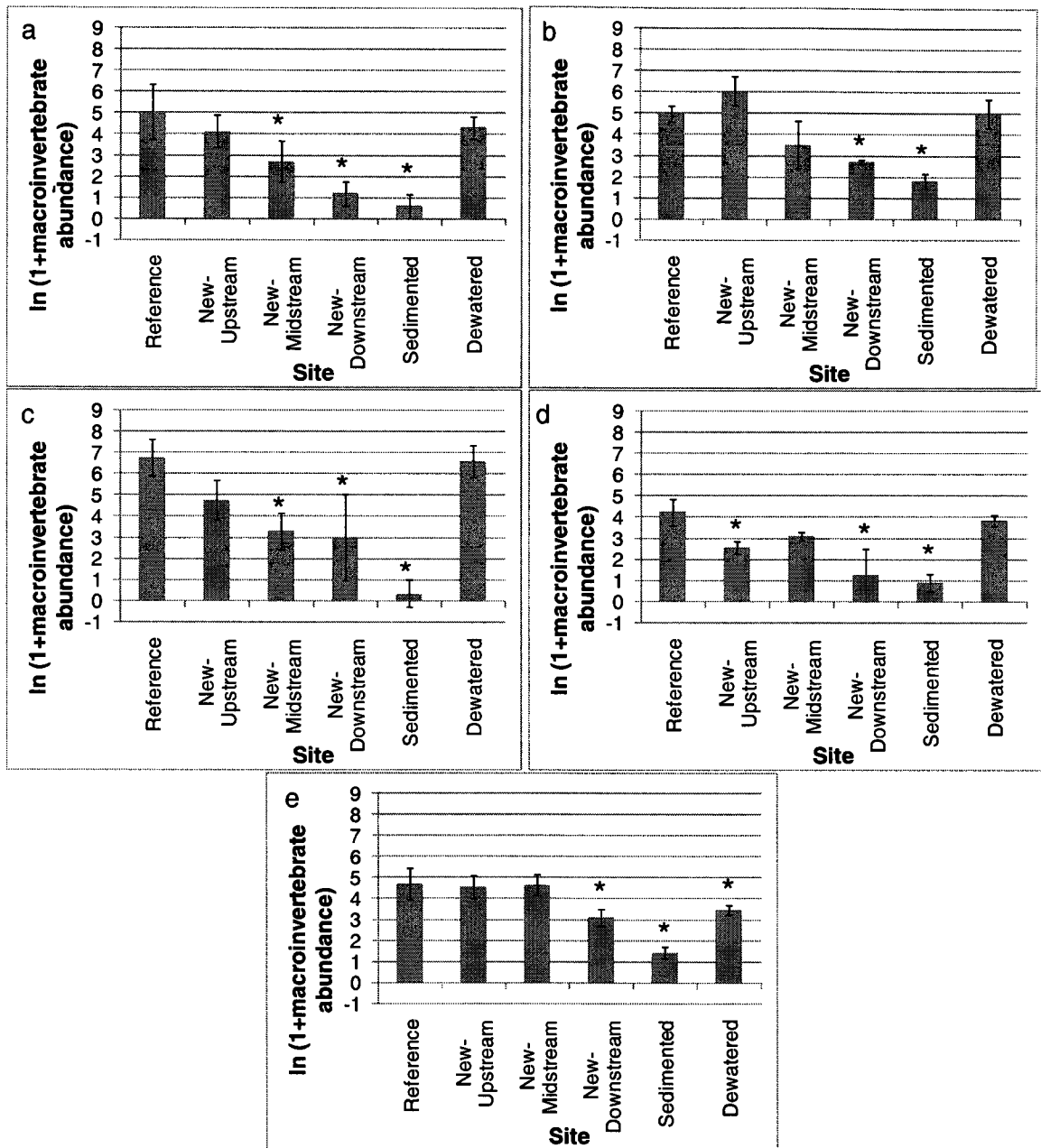


Figure 2.6. Log-transformed macroinvertebrate abundance per kicknet sample (mean \pm 1 SD) at sample sites. One-way Anova was used to examine differences in macroinvertebrate abundance among sample sites on 7/12/06 ($R^2 = 80.0\%$; $F_{5,12} = 14.6$; $p < 0.001$; a), 9/29/06 ($R^2 = 84.3\%$; $F_{5,12} = 19.22$; $p < 0.001$; b), 2/10/07 ($R^2 = 78.5\%$; $F_{5,11} = 12.65$; $p < 0.001$; c), 5/15/07 ($R^2 = 79.7\%$; $F_{5,12} = 14.33$; $p < 0.001$; d), and 8/21/07 ($R^2 = 85.3\%$; $F_{5,12} = 20.73$; $p < 0.001$; e). Asterisks show significant differences at the 95% confidence level in comparison with the Reference site using Dunnett's comparisons.

Table 2.1. Model variables, coefficients, and p values for a regression model of macroinvertebrate abundance (adjusted $R^2 = 56\%$; $F_{2,27} = 10.10$; $p < 0.001$)

variable	coefficient	p
Total suspended sediment (mg/L)	-0.0390	0.013
Median particle size (mm)	0.0296	0.001

variation; 56.3% on axis 1 and 28.9% on axis 2 (Figure 2.7). A shift in community composition from the Reference and Dewatered sites (low scores on axis 1) to the sites within the new channel (intermediate scores on axis 1) to the downstream Sedimented site (high scores on axis 1) was associated with decreasing particle size and increasing suspended sediment levels. A seasonal shift in community composition from winter (low scores on axis 2) to fall (high scores on axis 2) was also associated with decreasing dissolved oxygen concentrations and increasing dissolved organic nitrogen concentrations. MRPP indicated highly significant ($A = 0.120$, $p < 0.0001$) differences in taxonomic composition among three groups of sites: 1) Reference and Dewatered, 2) New-Upstream, New-Midstream, and New-Downstream, and 3) Sedimented.

When fish were surveyed on 8/27/07, species richness was equal at all sampling locations, with eight species documented at each site. Catch per unit effort was slightly depressed in and downstream of the avulsion but elevated at the dewatered site as compared with the reference site (Figure 2.8a). This trend was nearly the same when YOY

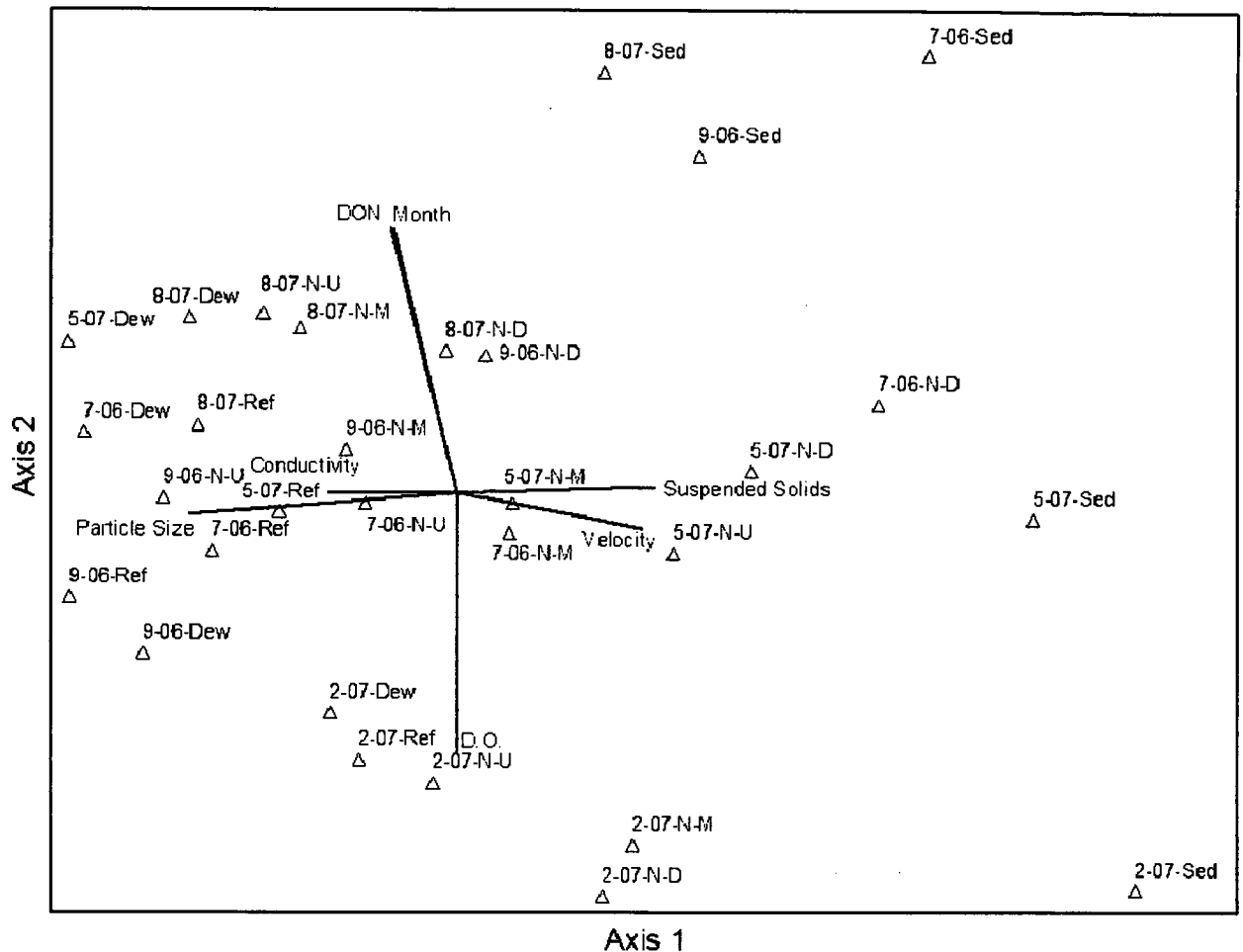


Figure 2.7. NMS ordination of macroinvertebrate sampling sites. Vectors portray direction and strength of Spearman rank correlations between explanatory variables and ordination axes. Codes are shown for sample sites and dates sampled as month-year-site for Reference, New-Upstream, New-Midstream, N-Downstream, Sedimented, and Dewatered sites.

fish were excluded from the analysis, except catch per unit effort was slightly elevated downstream of the avulsion in comparison with the reference site (Figure 2.8b). There were significant associations between fish communities and sampling sites both when YOY fish were included in the analysis ($\chi^2_{18} = 293.8$; $p < 0.001$) and when they were excluded ($\chi^2_{18} = 207.0$; $p < 0.001$; Figures 2.9 and 2.10). Longnose dace (*Rhinichthys*

cataractae) and redbreast sunfish (*Lepomis auritus*) were found only at the Reference site. Several species were not found at the Reference site but were found at one or more

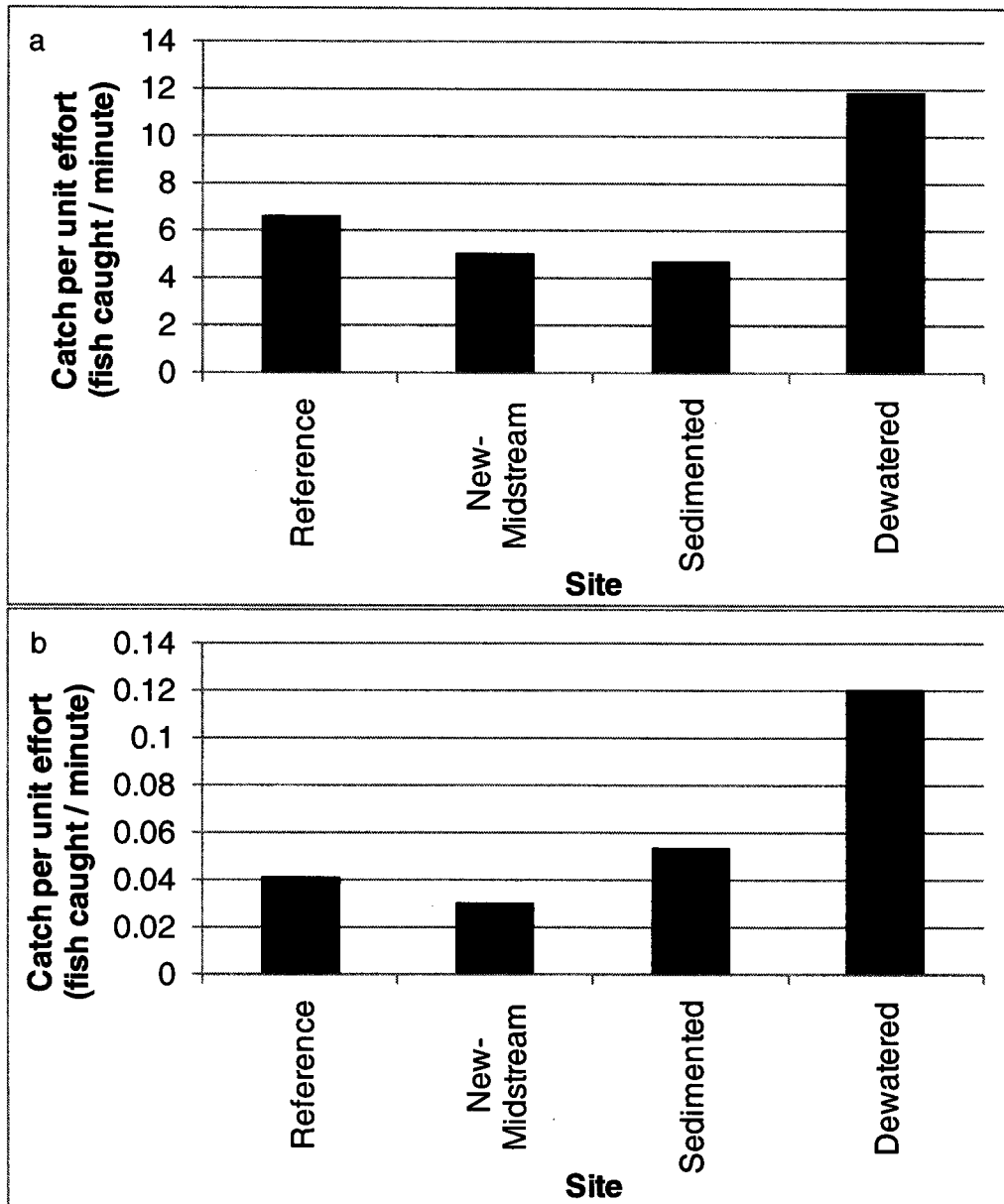


Figure 2.8. Total fish catch per unit effort in the Suncook River system 15 months after the avulsion including (a) and excluding (b) YOY fish

of the disturbed sites including yellow perch (*Perca flavescens*) at the New-Midstream site, brown bullhead (*Ameiurus nebulosus*) at the New-Midstream and Dewatered sites, and pumpkinseed (*Lepomis gibbosus*) at all three disturbed sites. The fish community at the New-Midstream site was dominated by young-of-year common white sucker (*Catostomus commersoni*), and the Dewatered site was dominated by margined madtom (*Noturus insignis*).

Whole-Stream Metabolism

GPP in the new and sedimented reaches was not significantly different from GPP in the reference reach (one-way ANOVA; $R^2 = 49.6\%$; $F_{2,3} = 3.46$; $p = 0.166$) when whole-stream metabolism was measured 17 months after the avulsion (Figure 2.11a). As shown in Figure 2.11b, GPP in the dewatered and reference reaches was also not significantly different when measured over three subsequent days (two-sample t-test; $t_3 = -1.31$; $p = 0.280$). On the other hand, R was significantly lower in both the new and sedimented reaches as compared with the reference site (one-way ANOVA; $R^2 = 96.8\%$; $F_{2,3} = 76.74$; $p = 0.003$), and R was also significantly lower in the dewatered reach as compared with the reference site (two-sample t-test; $t_3 = -6.74$; $p = 0.007$) as shown in Figures 2.11c and 2.11d, respectively. P/R was significantly higher in the new and sedimented reaches as compared with the reference site (one-way ANOVA; $R^2 = 95.2\%$; $F_{2,3} = 50.19$; $p = 0.005$), as shown in Figure 2.11e. As shown in Figure 2.11f, P/R in the dewatered and reference reaches were not significantly different (two-sample t-test; $t_3 = 1.13$; $p = 0.342$).

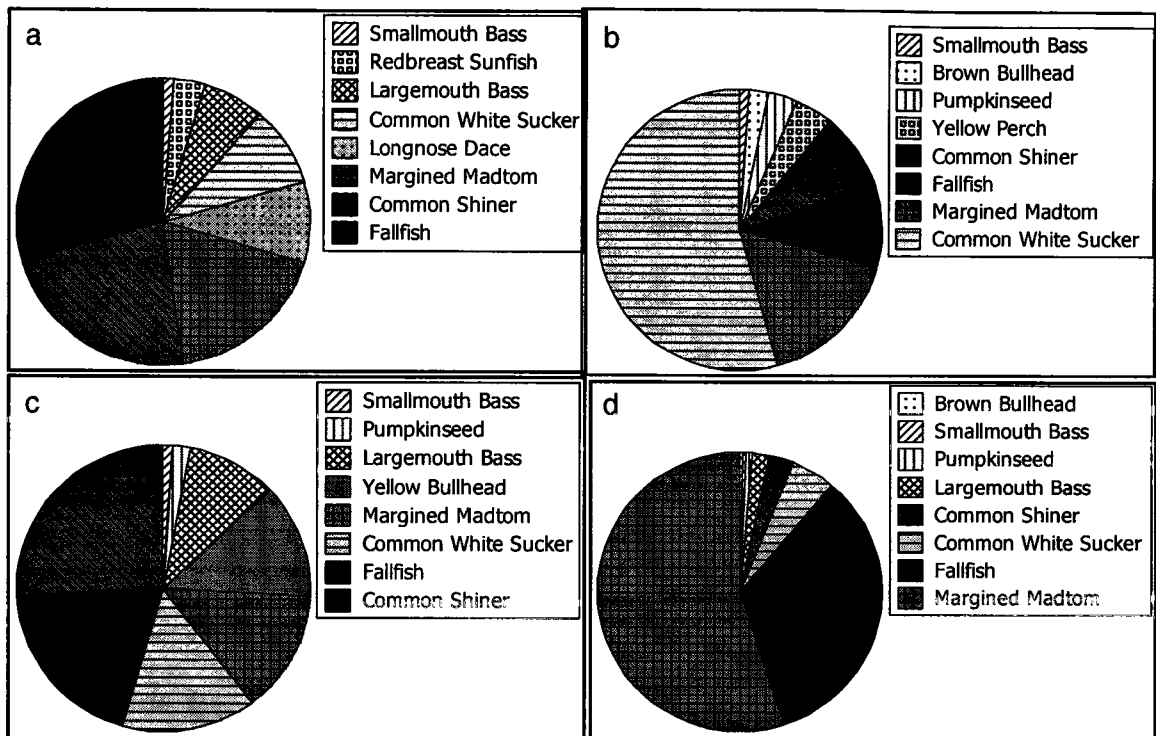


Figure 2.9. Fish community composition in the Suncook River system 15 months after the avulsion at the Reference (a), New-Midstream (b), Sedimented (c), and Dewatered (d) sites including YOY fish

Discussion

Geomorphology

The 2006 Suncook River avulsion dewatered a reach of approximately 2.5 km and carved out a new channel approximately 800 m in length. All of the Suncook River's flow was captured by this new channel, while the dewatered channel continued to be fed only by a small tributary. The incision of this new channel resulted in the export of massive amounts of fine sediment and blanketing of the streambed downstream of the new channel with sand. Following the avulsion, I documented dramatic changes in streambed substrate size, with median particle size declining from cobbles upstream of the avulsion and in the dewatered reach, to gravel in the new reach, to sand downstream

of the avulsed channel. Streambed substrate size in and downstream of the new channel showed no evidence of recovering to reference conditions when surveyed seventeen months after the avulsion.

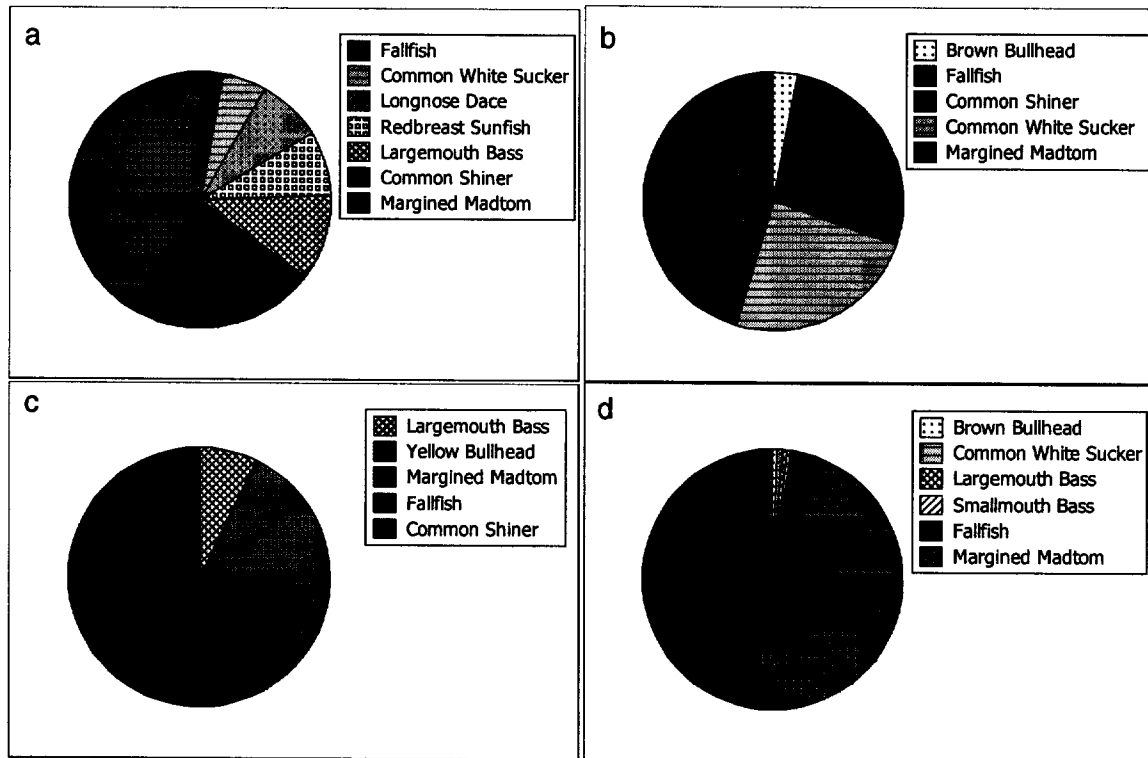


Figure 2.10. Fish community composition in the Suncook River system 15 months after the avulsion at the Reference (a), New-Midstream (b), Sedimented (c), and Dewatered (d) sites excluding YOY fish

While Wolman and Miller (1960) proposed that stream channel form develops as a result of frequent, moderate flows rather than large floods, Baker (1977) theorized that in some climatic and physiographic settings, the opposite would be true. Field studies have documented that, while some floods have little effect on stream channel form (Costa 1974, Moss and Kochel 1978), others can result in dramatic geomorphic changes

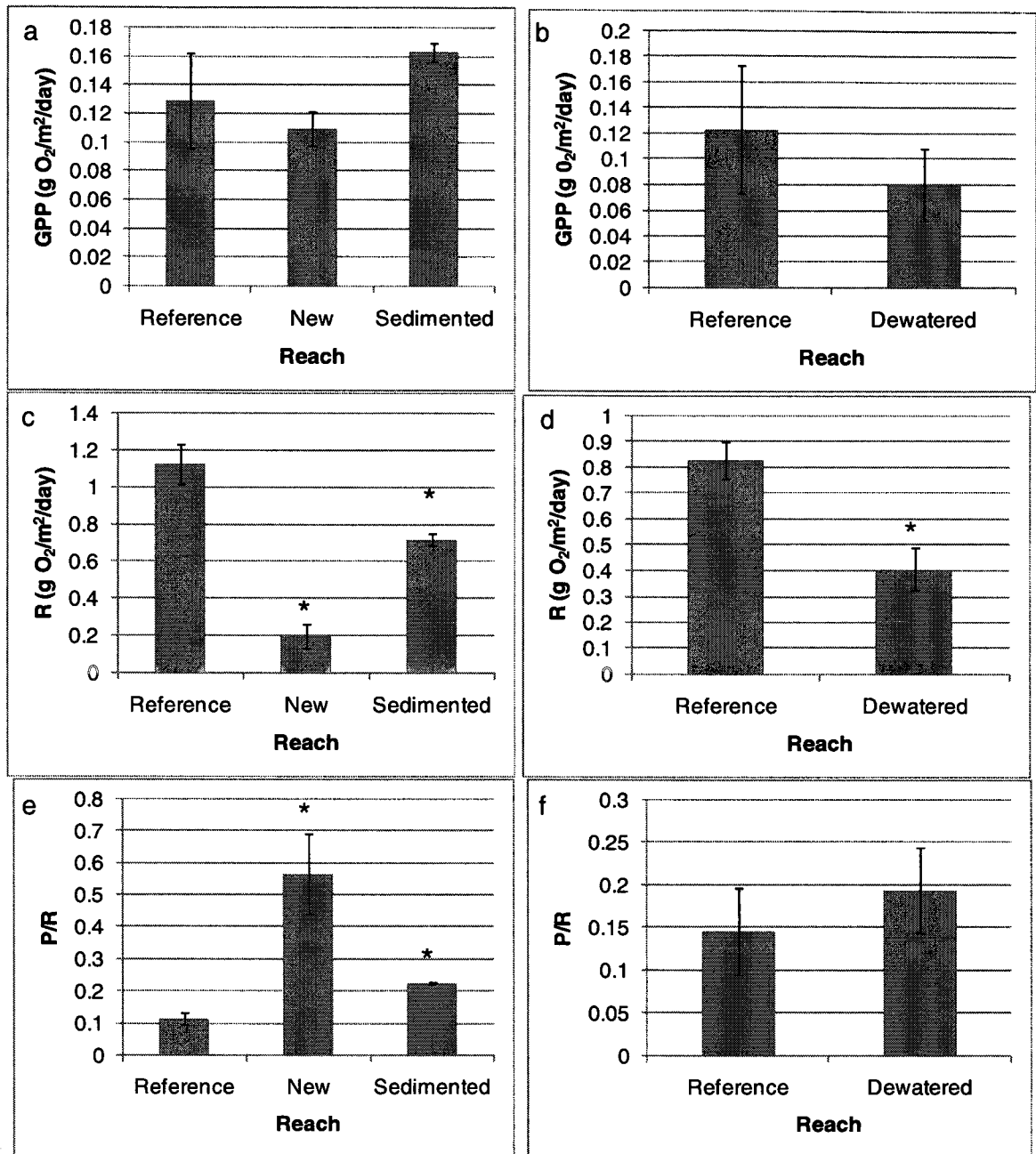


Figure 2.11. Whole-stream metabolism in the Suncook River new and sedimented reaches (a, c, e) and dewatered reach (b,d,f) in comparison with the reference site 17 months after the avulsion; asterisks show significant differences at the 95% confidence level in comparison with the reference reach using one-way ANOVA with Dunnett's comparisons (c and e) and a two-sample t-test (d).

(Desloges and Church 1992, Lapointe et al. 1998, Greenbaum and Bergman 2006, Smith et al. 2006, McEwen and Werritty 2007). Similar to the Suncook River avulsion, Lapointe et al. documented how an avulsion of the Ha! Ha! River in Quebec resulted in the aggradation of sand downstream of the newly incised channel (1998), and these authors highlighted the potential for scour and sedimentation (and potentially severe impacts on infrastructure) in other glaciated valleys.

The duration of large geomorphic changes following flood events is variable. Greenbaum and Bergman (2006) documented the evacuation of a large gravel bar within four years of the flood that formed it in a Mediterranean ephemeral stream in Israel. Geomorphic impacts of floods in ice-marginal settings in Iceland and British Columbia have been estimated to last for years to decades (Smith et al. 2006) and decades to a century (Desloges and Church 1992), respectively. In Scotland, sediment deposition from a large flood was still apparent 145 years later (McEwen and Werritty 2007).

Water quality

Studies have shown that, while the relationship between discharge and suspended sediment concentration during flood events is complex, in general a positive relationship exists between these two variables (Lefrancois et al. 2007, Zabaleta et al. 2007).

Sediment availability also drives sediment delivery and is a major factor contributing to the complexity of the relationship between discharge and concentration of suspended solids (Lefrancois et al. 2007, Zabaleta et al. 2007). In the Suncook River, suspended sediment concentrations in and downstream of the new channel declined over approximately two months following the avulsion. This trend likely reflects reductions in

both discharge and in-stream sediment availability. In comparison to reference conditions, suspended sediment concentrations continued to exhibit greater variability in and downstream of the new channel throughout the study period, probably due to the massive quantity of in-stream fine sediment that became available at those sites following the avulsion.

Following the avulsion, water quality parameters including temperature, dissolved oxygen, and concentration of nutrients and ions in and downstream of the new channel were not notably different from conditions at the reference site. On the other hand, concentrations of major ions and of nitrate were markedly higher in the dewatered channel, which continued to be fed by Mason Brook. Over the study period, specific conductance of Mason Brook was, on average, 3.5 times greater than at the reference site. As soon as the new channel captured the Suncook River's flow, stream flow inputs from this small tributary were no longer diluted, and specific conductance in the dewatered channel immediately approached that of Mason Brook. Reduction of flow (and corresponding lack of dilution) also probably led to the elevated nitrate concentrations measured in the dewatered channel following the avulsion. Nitrate concentrations measured in the dewatered channel were consistently the highest amongst all sampling sites (including Mason Brook), likely due to nutrient inputs from an adjacent cornfield. Several other studies have documented increased conductivity resulting from reduced dilution under low flow conditions (Caruso 2002, Zwolsman and van Bokhoven 2007), though these studies emphasized increased groundwater inputs, evaporation, and influence of effluent point sources, rather than increased influence of headwater streams leading to increased conductivity. Sprague (2005) also documented increased nutrient

concentrations under drought conditions due to decreased dilution of irrigation return flow.

Biota

In and downstream of the avulsion, sedimentation led to a dramatic reduction in macroinvertebrate abundance. This reduction in macroinvertebrate abundance was significantly associated with both substrate size and suspended sediment concentration. Wood and Armitage (1997) noted several studies that have documented reductions in macroinvertebrate density following sedimentation and they described four ways that sedimentation affects macroinvertebrates: 1) through alteration of substrate composition; 2) through increased drift due to sediment deposition or reduced substrate stability; 3) by interfering with respiration structures and reducing of oxygen availability; and 4) by interfering with feeding by impeding filter-feeding, reducing food value of periphyton, or reducing prey availability. While studies have shown that sedimentation has led to reduced macroinvertebrate taxa richness (Lemly 1982), taxa richness is sensitive to total abundance of a sample. Several studies using ordination techniques to investigate effects of sedimentation on macroinvertebrate assemblages have found macroinvertebrate communities to be resistant to this type of disturbance (Kreutzweiser et al. 2005, Thomson et al. 2005), suggesting that prior evidence of reductions in macroinvertebrate taxa richness associated with sedimentation (Lemly 1982) may have been due to sample size effects. The results of this study indicate that sedimentation may lead to changes in both macroinvertebrate abundance and community composition.

Macroinvertebrate abundance in the dewatered channel was comparable to the reference site until the last sampling date, when it declined slightly. It is unknown whether this result was an anomaly, or whether it signaled a delayed response to low-flow conditions. Other studies have documented that the response of macroinvertebrate abundance to reduced flow conditions is variable, sometimes declining due to reduced habitat area and food quality and ensuing changes in competition and predation, and sometimes increasing due to concentration within a smaller wetted area or changes in habitat suitability or food resources (Dewson et al. 2007b). Changes in macroinvertebrate abundance and community structure due to dewatering have also been shown to be dependent on water quality conditions, with lower quality streams showing no response to dewatering (Dewson et al. 2007a).

Fifteen months after the avulsion, total fish catch per unit effort was slightly depressed in and downstream of the new stream reach, where the channel was severely sedimented and where benthic macroinvertebrate abundance was markedly depressed. On the other hand, catch per unit effort was notably higher in the dewatered reach. Prior research suggests that fish abundance generally declines due to dewatering (Haxton and Findlay 2008). The increase in fish abundance observed at the dewatered site may be an indirect effect of the avulsion, which led to elevated nitrate concentrations at this site. Several studies have documented bottom-up effects of nutrient enrichment in stream environments (Peterson et al. 1993b, Askey et al. 2007). Alternatively, constriction and fragmentation of stream habitat may have simply concentrated fish into a smaller area (from which they were easier to catch). Changes in fish communities also reflected species-specific habitat preferences. Longnose dace, which prefer coarse substrates of

fast-moving streams (Page and Burr 1991), were only found at the reference site, whereas brown bullhead, which prefer pools and slow-moving runs over soft substrates (Page and Burr 1991), were only found in the new and dewatered channels. The new channel was dominated by young-of-year common white sucker, which is a generalist species that occupies a full range of habitats from rocky riffles to large lakes (Page and Burr 1991).

Whole-Stream Metabolism

As quantified following the avulsion, the Suncook River system was highly heterotrophic, with R much greater than GPP at all sampled locations. The avulsion apparently led to lower R in and downstream of the new reach and in the dewatered channel, while GPP was not significantly altered. In and downstream of the new channel, P/R was significantly greater than at the reference site, though this ratio was not significantly altered in the dewatered channel. Houser et al. (2005) also found that disturbance that led to high levels of sedimentation resulted in lowered R but no discernible effect on GPP. They suggested that reductions in R were due to burial of coarse woody debris that would otherwise help form debris dams that may act as respiration hot spots in streams, which may also be the case in and downstream of the new Suncook River channel. Dahm et al. (2003) suggested that drought conditions generally favor autotrophy due to reduced DOC inputs and a decreased ratio of organic : inorganic nutrient inputs. Although R did decline in the dewatered Suncook River channel, DOC concentrations remained slightly elevated at this site throughout the study period, and DON concentrations were not discernibly lower than reference conditions.

Conclusion

The May 2006 Suncook River flood and avulsion resulted in major changes to in-stream habitat and ecology over the short and long-term. While dramatically high levels of suspended sediment in and downstream of the new channel recovered to background conditions within approximately two months, over the long term the avulsion resulted in greater variability in suspended sediment concentrations and a shift in substrate size from cobbles to sand in these reaches. This was, in turn, associated with a persistent decline in macroinvertebrate abundance, altered macroinvertebrate and fish communities, and depressed whole-stream respiration. Dewatering resulted in long-lasting changes to water chemistry due to reduced dilution of a tributary and of an agricultural source. Dewatering also led to changes in the fish community and a reduction in whole-stream respiration. While sedimentation is appreciated as a common threat to streams following landscape disturbance and dewatering is a growing threat due to increased water withdrawals, both conditions are involved in the complex way a river responds to an avulsion. If changing climate conditions lead to an increased rate of river avulsions, particularly in glaciated river valleys, a better understanding of geomorphic conditions that precede avulsions and ecosystem effects that follow may become increasingly important in managing water resources.

CHAPTER 3

INFLUENCE OF STABLE REFUGIA AND PHYSICAL DISTURBANCE ON WHOLE-STREAM METABOLISM AND BENTHIC MACROINVERTEBRATE COMMUNITIES IN HEADWATER STREAMS

Abstract

The influence of altered disturbance regimes and reduced availability of refugia on macroinvertebrate communities and stream ecosystem function at the reach-scale is poorly understood. This chapter reports the results of a field experiment that examined the individual and combined effects of reduced streambed stability and removal of large rocks from the streambed on benthic organic matter, periphyton, macroinvertebrate communities, and whole-stream metabolism. While increasing the frequency of streambed disturbance without altering stream substrate composition had minimal impact on macroinvertebrate and whole-stream metabolism metrics, large streambed rocks appear to be very influential in maintaining stream ecosystem structure and function. Further, this research indicates that the presence of refugium stones is especially important in streams exposed to increased physical disturbance frequency.

Introduction

Alteration of stream substrate stability is a widespread phenomenon due to the increasing amount of impervious surface area in urbanizing watersheds. Larger peak flows following storm events in these urbanizing watersheds are more likely to result in

movement of the streambed. Studies have documented a negative relationship between watershed impervious surface area and stream metabolism (Young and Huryn 1999, Houser et al. 2005, Bott et al. 2006). To date, studies examining the relationship between urbanization and whole-stream metabolism have used correlation to infer causation; there is a paucity of research experimentally examining the relationship between substrate stability and whole-stream metabolism. At the reach-scale, reduced substrate stability is one mechanism by which urbanizing watersheds with increased impervious surface areas may alter stream ecosystem structure and function.

Lake et al. (2007) reviewed how different types of refugia are necessary for persistence of aquatic organisms following different types of disturbances. They proposed that stream restoration efforts would benefit from restoration of refugia in order to maintain aquatic communities in environments exposed to continuing anthropogenic disturbance. The relationship between altered disturbance regimes and the availability of refugia in maintaining macroinvertebrate communities at the reach scale has not been established. Even less attention has been focused on the degree to which refugia contribute to the maintenance of stream ecosystem function.

In lotic systems, gross primary production (GPP) represents the production of organic compounds from inorganic carbon by stream autotrophs. Ecosystem respiration (R) encompasses the in-stream consumption of organic compounds produced both within (autochthonous) and outside (allochthonous) of the stream. Together, GPP and R are referred to as “whole-stream metabolism.” Houser et al. (2005) documented low and temporally variable whole-stream GPP in sandy-bottomed streams in which frequent resuspension and redistribution of sediments likely limited the development of primary

producer communities. Sediment instability has been shown to lead to reductions in periphyton biomass, with smaller, less stable sediments from lake inlet reaches supporting less periphyton biomass as compared with larger, more stable sediments from lake outlets (Myers et al. 2007). Biggs et al. (1999) found that mean chlorophyll *a* concentrations were higher on stable substrates than on unstable sediments. They also found that chlorophyll *a* maxima occurred on unstable sediments (as measured by frequency of bed movement) after periods of low flow, while stable substrates exhibited more regular, long-term trends in chlorophyll *a* concentrations.

Physical disturbance can influence macroinvertebrate abundance and diversity both directly and indirectly. Floods can dislodge organisms from the streambed, with some taxa more likely to become dislodged than others, depending on a variety of adaptations. Floods can also scour periphyton from the stream bed, reducing available food resources for macroinvertebrates. Finally, floods can alter stream habitat characteristics, which in turn affect colonization by periphyton and by macroinvertebrates. Although a number of mechanisms have been proposed to explain the relationship between disturbance frequency and macroinvertebrate diversity in streams, the intermediate disturbance hypothesis (Connell 1978) has probably received the most attention. Unfortunately, results of most field studies do not conform to predictions derived from this framework (Vinson and Hawkins 1998). Death (2002) proposed an alternative mechanism, suggesting that higher levels of primary productivity result in greater periphyton biomass in streams which, in turn, leads to greater species richness. At low levels of productivity, macroinvertebrates are more likely to leave the system by drifting. At high levels of productivity, on the other hand, macroinvertebrates

are less likely to drift, thereby remaining in the system and contributing to increased species richness.

Large rocks can act as refugia for periphyton (Uehlinger 1991) and macroinvertebrates (Matthaei et al. 2000) when the benthos is physically disturbed in a patchy manner. Matthaei et al. (2000) found that large surface stones act as refugia for macroinvertebrates during hydrologic disturbances. They propose that macroinvertebrates may actively seek large refugium stones from which they recolonize unstable streambed patches following high flow events. Theoretically, in stream reaches exposed to higher frequencies of disturbance, the importance of large stones in maintaining macroinvertebrate communities and whole-stream metabolism should increase.

Large rocks may also influence stream metabolism by altering near-bed hydraulics. Cardinale et al. (2002) found that stream metabolism was reduced in response to increased uniformity of substrate size, likely due to changes in near-bed hydraulic conditions. Altered hydraulics may change the supply rate of nutrients, gases, and organic matter to periphyton, thereby directly altering metabolism. Changes in hydraulics may also indirectly affect metabolism by altering periphyton species composition. Thus, even in less frequently disturbed stream reaches, the presence of large substrate particles may maintain higher rates of whole-stream metabolism due to alterations in near-bed hydraulic conditions.

Schindler (1987) wrote, “Few single ecosystem-level studies of perturbation have incorporated a broad variety of organizational, nutrient-cycling, and energy-flow aspects; thus it is impossible to compare them.” While functional metrics are now being proposed for use as indicators of ecosystem disturbance in lotic systems (Bunn et al. 1999, Bott et

al. 2006, Young et al. 2008), studies that simultaneously measure the response of both structural and functional metrics to stream perturbations are still rare. Thus, we are still unable to compare the utility of structural and functional metrics as indicators of different types of ecosystem disturbance. This research simultaneously assesses whole-stream metabolism and macroinvertebrate community metrics in order to compare these two approaches and the degree to which they reflect physical ecosystem disturbance over time.

I present the results of a field experiment that examined the individual and combined effects of reduced streambed stability and removal of large rocks from the streambed on benthic organic matter, periphyton, macroinvertebrate communities, and whole-stream metabolism. I hypothesized that reductions in streambed stability would lead to reduced periphyton, macroinvertebrate diversity, and rates of whole-stream metabolism and that the presence of large stones would contribute to maintaining these parameters.

Methods

Study area

This experiment was carried out on four small streams between May 21st and November 4th, 2008. Two of the streams were located within the Williams College Hopkins Memorial Forest in northwestern Massachusetts, and the other two streams were located on privately-owned land adjacent to Hopkins Forest in southwestern Vermont. All four streams were high gradient (5% to 9% slope) and relatively pristine; the Vermont stream watersheds were composed entirely of mixed hardwood forest, and the

Massachusetts stream watersheds were composed of mixed hardwood forest and open fields. Northern two-lined salamanders (*Eurycea bislineata*) were observed in all four streams, and fish were observed in two of the four streams. A forested 320 m reach without tributary inputs was selected on each stream. Median streamflow among study streams ranged from 2.3 to 15.0 L/s (as measured in this study). Between June and October, 2008, approximately 63.5 cm of rain fell in the study area (National Climatic Data Center records for Albany, NY). Average channel widths ranged from 1.2 m to 1.9 m and average channel depths ranged from 1.6 cm to 5.8 cm. Streams were dominated by coarse gravel (median particle size ranged from 16 mm to 56 mm).

Experimental Section

To test the above hypotheses, the four small streams described above were each divided into four 80-m-long experimental reaches from upstream to downstream (Table 3.1). Baseline data were collected before the experimental reaches were manipulated.

Table 3.1. Description of experimental treatments

Experimental reaches (beginning upstream)	Label	Treatment
0 – 80 m	C	Control
80 – 160 m	R	Removal of large refugium stones
160 – 240 m	D	Bi-weekly disturbance of streambed
240 – 320 m	RD	Removal of large refugium stones and bi-weekly disturbance of streambed

For each stream, whole-stream metabolism was determined simultaneously within each of the four experimental reaches using the upstream-downstream diurnal dissolved oxygen change technique (Marzolf et al. 1994) with the modification suggested by Young and Huryn (1998) for calculating the air-water exchange rate of oxygen. Temperature and dissolved oxygen concentrations were logged at 5-minute intervals for a minimum of 24 hours at the upstream and downstream end of each experimental reach with YSI 556 multiprobe systems and a YSI 600 XLM sonde (YSI, Yellow Springs, OH, USA). Reaeration coefficients, stream velocity, and discharge were determined based on the decline of dissolved propane concentration during a simultaneous, continuous injection of propane and NaCl (a conservative tracer) over each 80-m reach simultaneous with oxygen measurements. In the event that propane evasion was not detected over a single reach, reaeration was calculated to include an additional one or more 80-m reaches upstream, moving sequentially upstream until propane evasion was detectable. The rate of air-water O₂ exchange was calculated based on this calculated reaeration rate and the average of the oxygen saturation deficit or excess at both ends of the reach. The difference in dissolved oxygen between the ends of the reach was corrected for air-water O₂ exchange to calculate the net rate of dissolved oxygen change due to ecosystem metabolism at 5-minute intervals. Nighttime R was calculated as the sum of net ecosystem metabolism occurring at night, and daytime R was calculated by interpolating between average net ecosystem metabolism during the 30 minutes before dawn and after dusk. Total daily R was calculated as the sum of nighttime and daytime R rates over 24 hours (midnight to midnight), and daily GPP was calculated as the sum of the differences

between estimated daytime respiration rates and net ecosystem metabolism. P/R was calculated as the ratio of GPP to R.

Temperature and pH were logged at 5-minute intervals simultaneous with the measurement of stream metabolism. Average stream width and depth were determined by establishing transects every 10 m along each reach. PAR was monitored at two streamside locations in each reach during the period of oxygen measurements. Streamwater samples were filtered in the field using pre-combusted glass fiber filters (0.7 μ M pore size), and frozen until analysis. Cation (Na^+ , K^+ , Ca^{2+} , and Mg^{2+}), and anion (NO_3^- , Cl^- , SO_4^{2-} , and F^-) concentrations were measured using ion chromatography. Standard colorimetric methods were used to quantify concentrations of ammonium (EPA 1983b) and phosphate (EPA 1983a). Stratified Wolman (1954) pebble counts (Kondolf 1997) were carried out to characterize coarse surface substrate. Intermediate axes were measured using a meter stick or hand-held gravel analyzer (Gravelometer, US SAH-97, Wildlife Supply Company, Buffalo, NY) for at least 100 particles.

Following stream metabolism measurements, three replicate samples of benthic macroinvertebrates, benthic organic matter (BOM), and epilithon (for chlorophyll *a* determination) were collected from riffle-type habitats within each reach. Benthic macroinvertebrates and BOM were collected using a kicknet (46 cm wide by 23 cm tall with a mesh size of 500 μ m) and disturbing the streambed within 30 cm upstream of the net. Samples were preserved in 70% ethanol, and macroinvertebrates were identified to the family level. Remaining detritus was dried at 60°C, weighed, combusted at 450°C for four hours, and reweighed to determine ash-free dry mass of BOM. Epilithon was collected by gathering a sufficient number of representative rocks from the stream bottom

to fully cover a 433 cm² tray. Epilithon was scrubbed from the rocks with a brush and the slurry was collected and frozen. Frozen slurry samples were thawed and filtered through a glass fiber total suspended solids filter in the laboratory and then filters and epilithon retentate were refrozen until analysis. Care was taken to work with epilithon samples in low light and to store them in the dark to minimize degradation of chlorophyll. Chlorophyll *a* was quantified by hot ethanol extraction followed by spectrophotometric analysis, according to the method of Sartory and Grobbelaar (1984).

The manipulations described in Table 3.1 were carried out beginning June 12, 2008 and continued through November 4, 2008. Rocks that appeared to be larger than the median (as determined from initial pebble counts) were removed from R and RD reaches. After the initial removal of large rocks from R and RD reaches, the entirety of the wetted channel of each 320 m stream reach was physically disturbed in order to equalize the impact of the initial disturbance among all experimental reaches; a team of four people walked the entirety of the channel and disturbed the streambed by foot to a depth of approximately 10 cm. Large rocks in R and RD reaches were not intentionally altered following this initial manipulation. Twice per week, D and RD reaches were physically disturbed by foot by one person in the manner described above. Approximately every six weeks, whole-stream metabolism was measured and macroinvertebrate, BOM, and epilithon samples were collected as described above. During the last month of the field experiment, the D reaches of the two Massachusetts streams were physically disturbed only once per week rather than twice per week due to the error of a field technician.

Data analysis

Masses of the three BOM samples collected from each experimental reach during each sampling round were averaged. Chlorophyll *a* masses of the three replicate epilithon samples from each reach were averaged in the same way. Macroinvertebrate abundance was determined as the total number of individuals collected in all three replicate samples from each reach. Macroinvertebrate family richness was summed over the three replicate samples from each reach in the same manner. Rarefied family richness was calculated in order to compare taxa richness among samples of varying sizes independent of the passive increase in taxa richness associated with larger sample sizes. For each samples, rarefied family richness was calculated according to Hurlbert (1971) as the expected number of families if that sample were the size of the smallest sample (54 individuals) as follows, where F is the number of families in a sample, N is the total number of individuals in a sample, N_i is the number of individuals in the i^{th} family, and n is the number of individuals in the smallest sample:

$$E(F) = \sum_{i=1}^F \left(1 - \left[\frac{\binom{N - N_i}{n}}{\binom{N}{n}} \right] \right)$$

Except for family richness and rarefied family richness, the above parameters, along with GPP, R, and GPP/R were log-transformed for statistical analysis. For each of the three post-manipulation sampling rounds, two-way ANOVA with stream as a blocking factor was used to test the main and interactive effects of substrate instability and absence of large streambed stones on the differences between post-disturbance values

and baseline measurements of each of the above parameters. One-way ANOVA with stream as a blocking factor and Dunnett's comparisons were used to compare differences in changes of the above parameters between each combination type of manipulated reach (R, D, and RD) and the control reaches.

Results

Experimental manipulation significantly reduced d_{84} particle size in reaches from which large stones were removed. As shown in Figure 3.1a, at the beginning of the experiment the difference in d_{84} particle size between reaches from which large stones were removed and those in which they were not altered was, on average, 70 mm (one-sided two-sample t-test; $t_9 = -4.36$; $p = 0.001$). As shown in Figure 3.1b, by the end of the experiment the difference in d_{84} particle size was, on average, reduced to 36 mm (one-sided two-sample t-test; $t_{10} = -4.43$; $p = 0.001$).

The experimental treatments did not significantly change BOM ash-free dry mass during the study period (Figure 3.2). The streambed disturbance treatment resulted in a significant decrease in chlorophyll a during the second post-manipulation sampling round (two-way ANOVA; $F_{1,9} = 5.34$; $p = 0.0462$). "R" reaches also exhibited significantly reduced chlorophyll a during the final sampling round compared with control reaches (one-way ANOVA with Dunnett's comparisons; $p = 0.0391$), as shown in Figure 3.3.

A list of macroinvertebrates collected in this study is included as Table 3.2. Macroinvertebrate abundance was significantly reduced in response to removal of large stones during the first post-manipulation sampling round (two-way ANOVA; $F_{1,9} = 23.08$; $p = 0.0010$); declines in macroinvertebrate abundance in R and RD reaches were

significant in comparison to control reaches (one-way ANOVA with Dunnett's comparisons; R=C $p=0.0082$; RD=C $p=0.0042$), as shown in Figure 3.4. During the

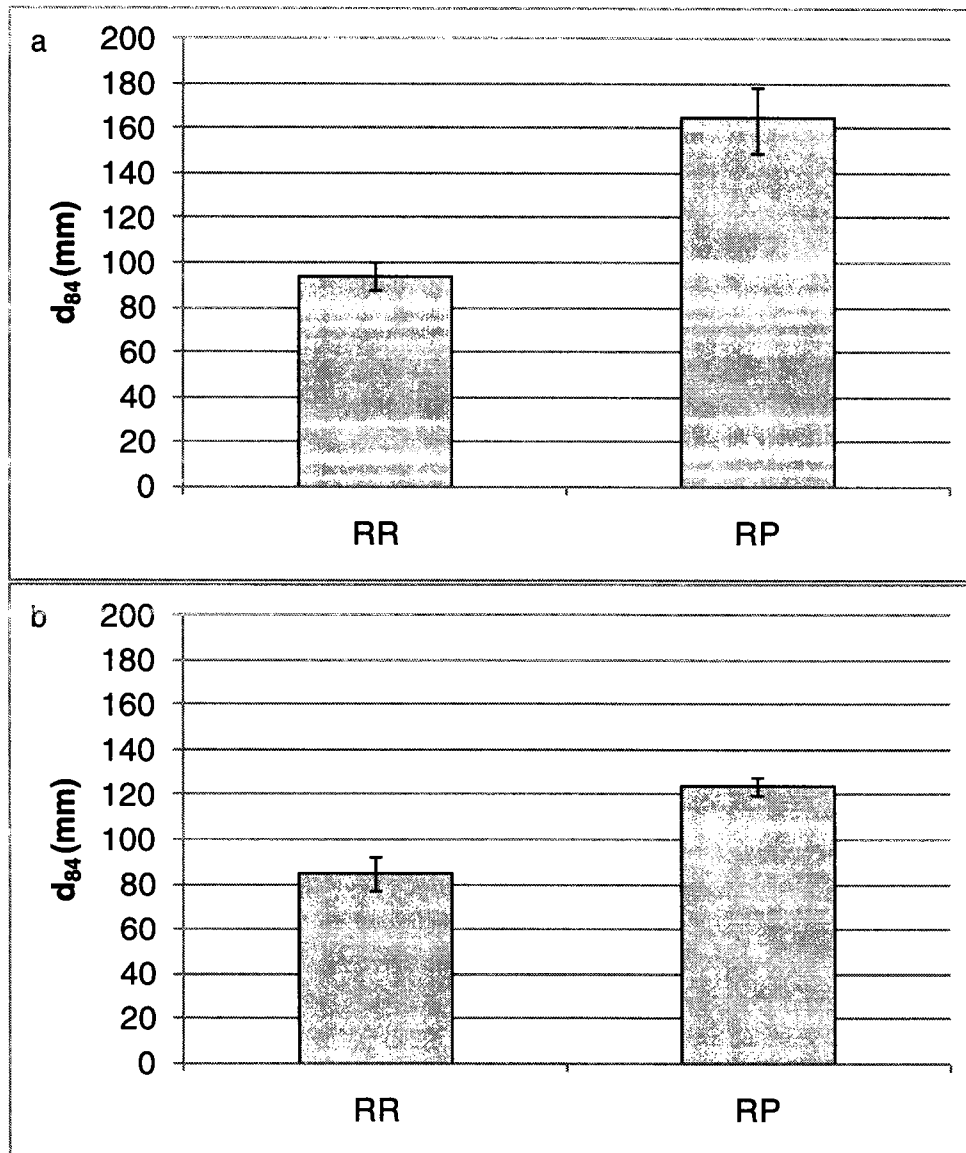


Figure 3.1. The d_{84} particle size in (N=8) reaches where large refugium stones were removed (RR) and (N=8) reaches where refugium stones were present (RP) at the start (a) and at the end (b) of the experiment. Columns show the means ± 1 SE.

second post-manipulation sampling round, macroinvertebrate abundance had declined significantly in response to the streambed disturbance treatment (two-way ANOVA; $F_{1,9}$

= 5.31; $p=0.0467$). During the final sampling round, macroinvertebrate abundance had declined significantly in RD reaches in comparison with control reaches (one-way ANOVA with Dunnett's comparisons; $p=0.0308$).

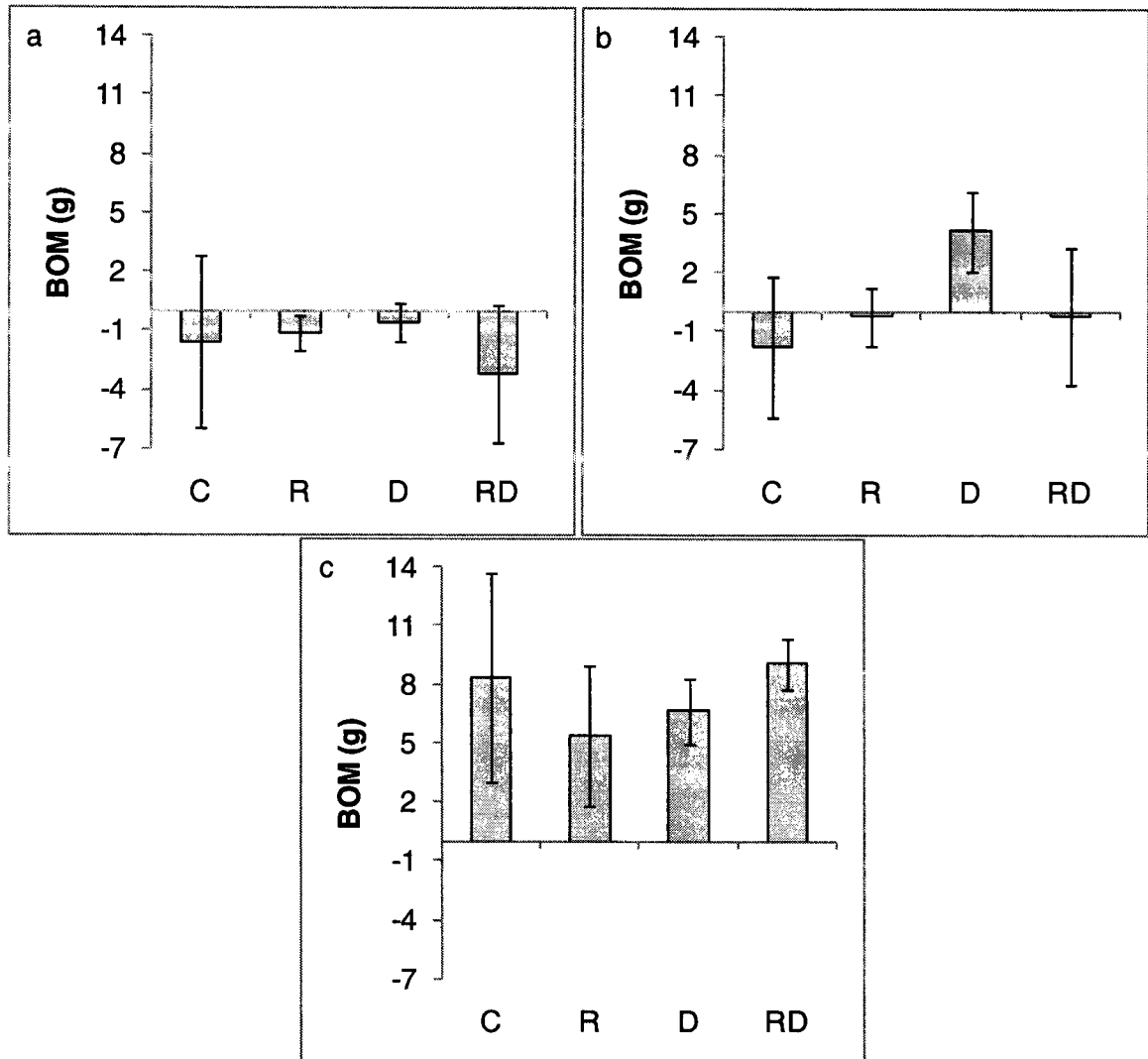


Figure 3.2. Differences between baseline measurements and post-disturbance values of ash-free dry mass of BOM in the four types of experimental reaches six (a) twelve (b) and eighteen (c) weeks after initiating treatments. Columns show mean differences \pm 1 SE.

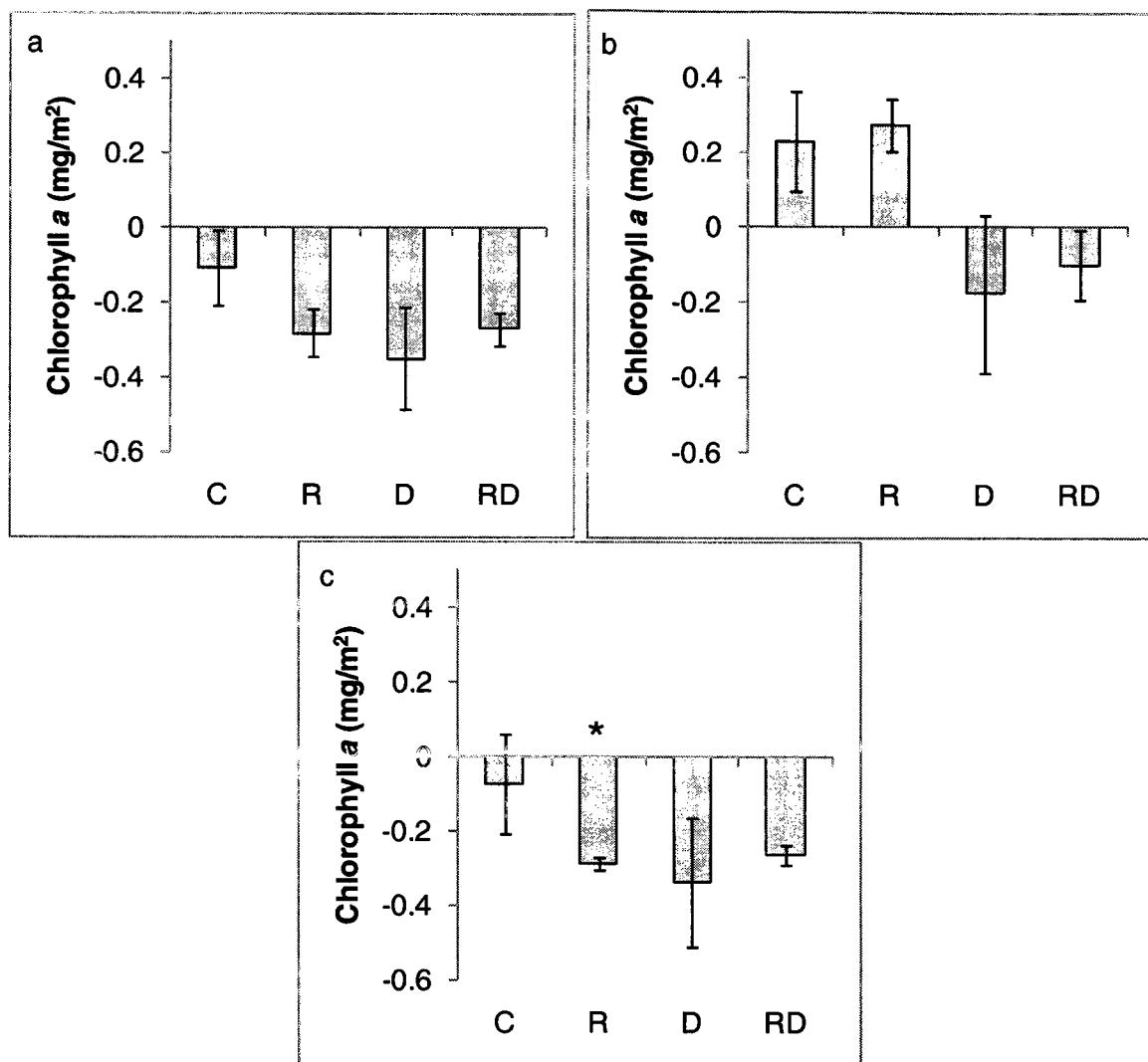


Figure 3.3. Differences between post-disturbance values and baseline measurements of chlorophyll *a* in the four types of experimental reaches six (a) twelve (b) and eighteen (c) weeks after initiating treatments. Columns show mean differences \pm 1 SE. Asterisk shows significant difference at the 95% confidence level in comparison with the control reaches using one-way ANOVA on log-transformed data with stream as a blocking factor and with Dunnett's comparisons.

Table 3.2. List of identified macroinvertebrate families

Order	Family	Order	Family
Coleoptera	Dytiscidae	Coleoptera	Halipilidae
Coleoptera	Elmidae	Coleoptera	Hydrophilidae

Table 3.2. List of identified macroinvertebrate families (cont.)

Order	Family	Order	Family
Coleoptera	Psephenidae	Megaloptera	Sialidae
Coleoptera	Ptilodactylidae	Nematomorpha	(unknown)
Diptera	Athericidae	Odonata	Gomphidae
Diptera	Ceratopogonidae	Oligochaeta	(unknown)
Diptera	Chironomidae	Plecoptera	Chloroperlidae
Diptera	Dixidae	Plecoptera	Leuctridae
Diptera	Dolichopodidae	Plecoptera	Nemouridae
Diptera	Empididae	Plecoptera	Peltoperlidae
Diptera	Psychodidae	Plecoptera	Perlidae
Diptera	Sciomyzidae	Plecoptera	Perlodidae
Diptera	Simuliidae	Plecoptera	Pteronarcyidae
Diptera	Stratiomyidae	Plecoptera	Taeniopterygidae
Diptera	Tabanidae	Trichoptera	Brachycentridae
Diptera	Tipulidae	Trichoptera	Glossosomatidae
Ephemeroptera	Baetidae	Trichoptera	Hydropsychidae
Ephemeroptera	Ephemerellidae	Trichoptera	Lepidostomatidae
Ephemeroptera	Heptageniidae	Trichoptera	Limnephilidae
Ephemeroptera	Leptophlebiidae	Trichoptera	Odontoceridae
Ephemeroptera	Siphonuridae	Trichoptera	Philopotamidae
Gastropoda	(unknown)	Trichoptera	Polycentropodidae
Gastropoda	Sphaeriidae	Trichoptera	Rhyacophilidae
Isopoda	Asellidae	Trichoptera	Uenoidae
Lepidoptera	Pyralidae		

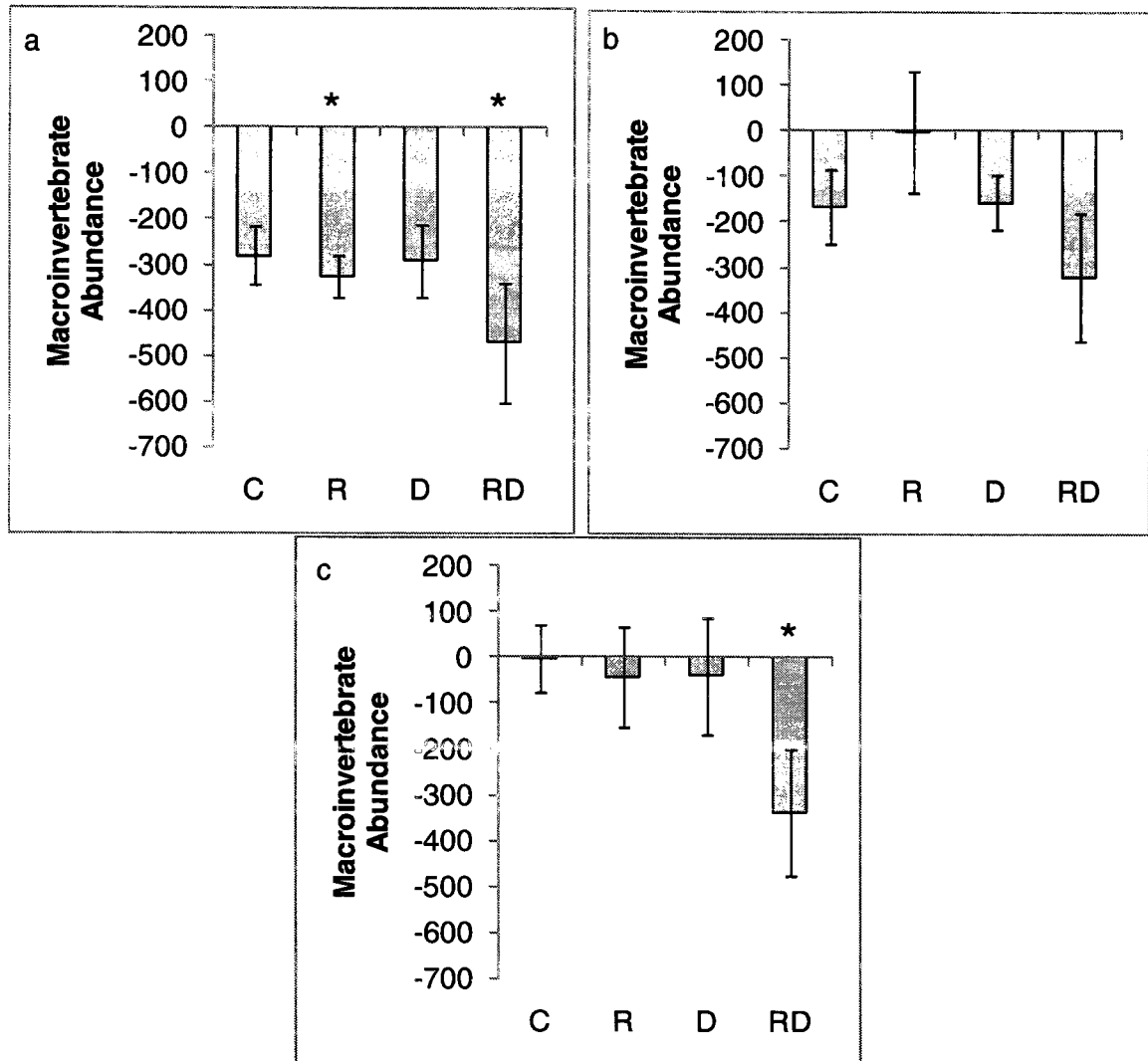


Figure 3.4. Differences between post-disturbance values and baseline measurements of macroinvertebrate abundance in the four types of experimental reaches six (a) twelve (b) and eighteen (c) weeks after initiating treatments. Columns show mean differences ± 1 SE. Asterisks show significant differences at the 95% confidence level in comparison with the control reaches using one-way ANOVA on log-transformed data with stream as a blocking factor and with Dunnett's comparisons.

During the second post-manipulation sampling round, an interaction between the two experimental treatments was significant in reducing family richness (two-way ANOVA; $F_{1,9} = 6.72$; $p = 0.0291$). During the final sampling round, removing large stones resulted in a significant decrease in family richness (two-way ANOVA; $F_{1,9} = 5.53$;

$p=0.0432$), and an interaction between the two experimental treatments was significant in reducing family richness (two-way ANOVA; $F_{1,9} = 8.05$; $p=0.0195$). Family richness appeared to be reduced in the RD reaches in comparison with control reaches during the final sampling round, but this effect was not statistically significant (Figure 3.5).

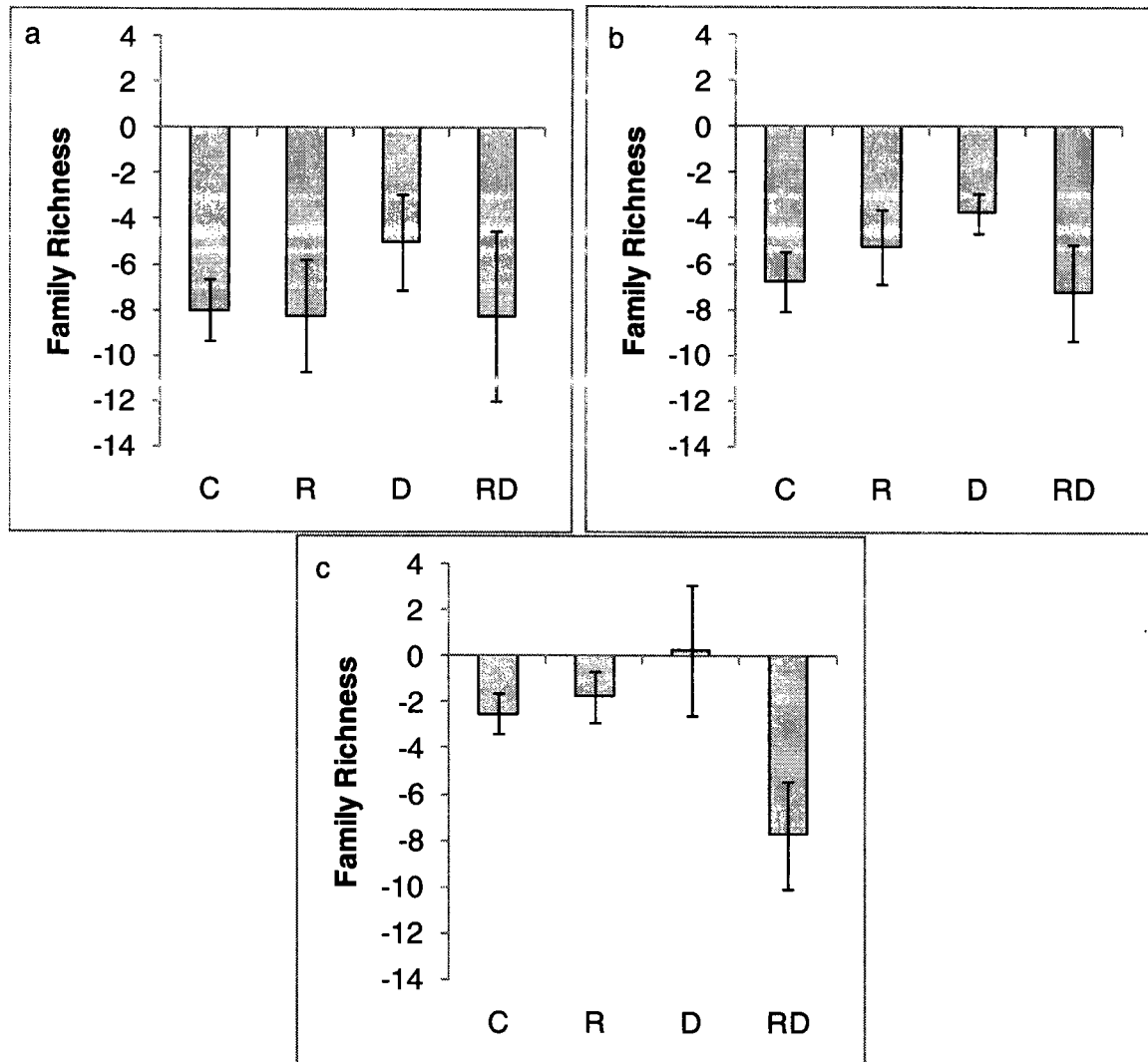


Figure 3.5. Differences between post-disturbance values and baseline measurements of macroinvertebrate family richness in the four types of experimental reaches six (a) twelve (b) and eighteen (c) weeks after initiating treatments. Columns show mean differences ± 1 SE.

During the second post-manipulation sampling round removing large stones led to significantly reduced rarefied richness (two-way ANOVA; $F_{1,9} = 11.78$; $p=0.0075$), and rarefied richness was significantly reduced in the RD reaches in comparison with control reaches (one-way ANOVA with Dunnett's comparisons; $p=0.0459$), as shown in Figure 3.6. During the final sampling round, an interaction between removing large stones and increasing frequency of streambed disturbance was significant in reducing rarefied family richness (two-way ANOVA; $F_{1,9} = 9.39$; $p=0.0135$).

Whole-stream metabolism was overwhelmed by rearing and could not be measured within several experimental reaches during each sampling round. Despite reduced sample sizes, several treatment effects were statistically significant. During the first post-manipulation sampling round, an interaction between the two treatments was significant in reducing GPP (two-way ANOVA; $F_{1,4} = 10.20$; $p=0.0331$). GPP appeared to be reduced in RD reaches during the first two post-manipulation sampling rounds, but these effects were not statistically significant (Figure 3.7). The experimental treatments did not significantly change R over the course of the study period, as shown in Figure 3.8.

During the first post-manipulation sampling round, an interaction between the two treatments was significant in reducing GPP/R (two-way ANOVA; $F_{1,4} = 28.83$; $p=0.0058$). During this initial post-manipulation sampling round, "R" reaches also exhibited significantly increased GPP/R compared with control reaches (one-way ANOVA with Dunnett's comparisons; $p=0.0195$), as shown in Figure 3.9. Significant treatment effects are summarized in Table 3.3a-c.

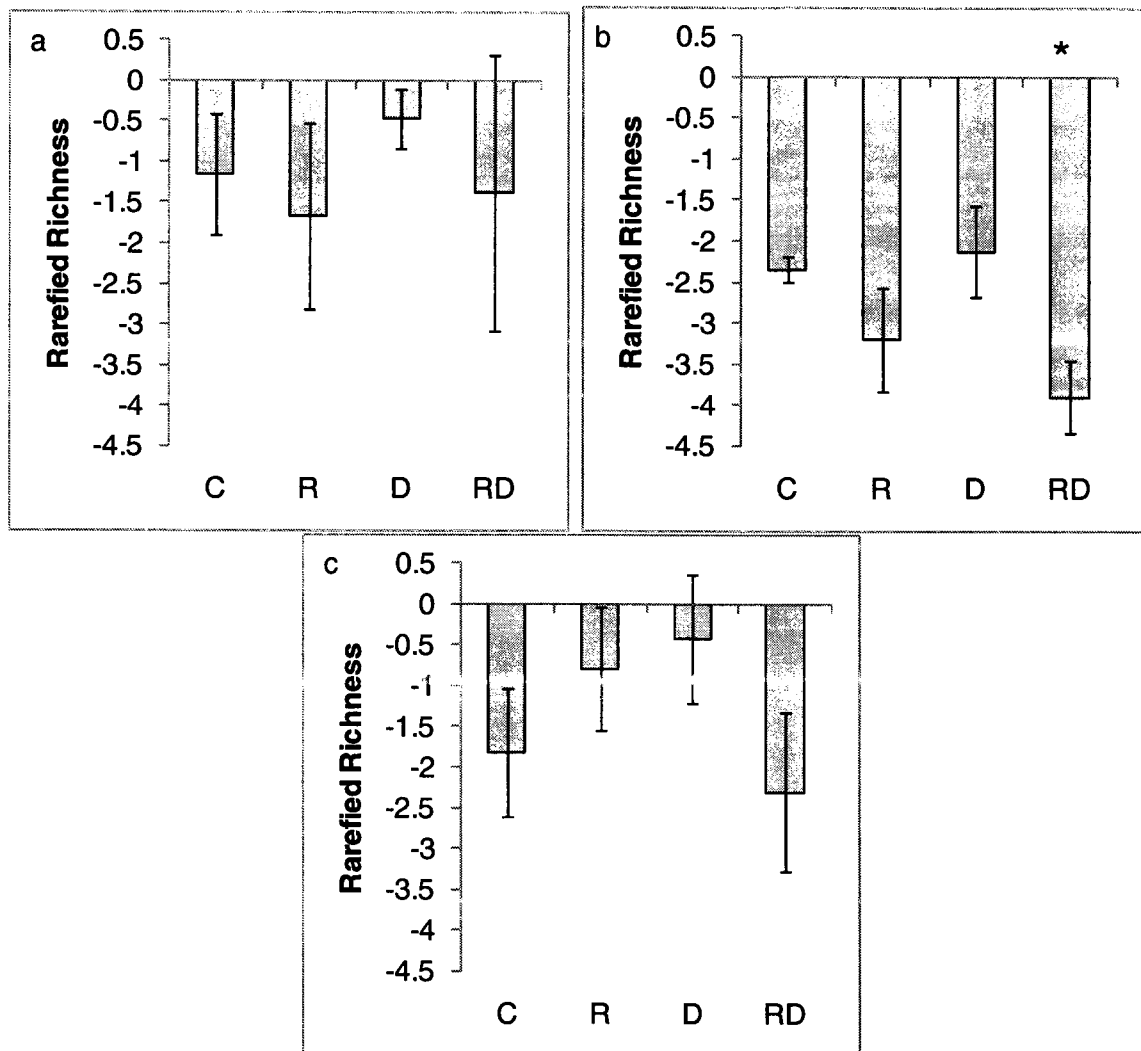


Figure 3.6. Differences between post-disturbance values and baseline measurements of rarefied macroinvertebrate family richness in the four types of experimental reaches six (a) twelve (b) and eighteen (c) weeks after initiating treatments. Columns show mean differences \pm 1 SE. Asterisk shows significant difference at the 95% confidence level in comparison with the control reaches using one-way ANOVA on log-transformed data with stream as a blocking factor and with Dunnett's comparisons.

Discussion

Increasing the frequency of streambed disturbance without altering stream substrate composition had minimal impact on ecosystem structure and function; the only

significant effect of increasing disturbance frequency was to reduce chlorophyll *a* and macroinvertebrate abundance during the second post-manipulation sampling round. Although experimental streambed disturbance treatments simulated bed-moving spates to some degree, these manipulations did not simulate the increased flows and suspended sediment loads that accompany natural bed-moving floods. In addition, while increasing

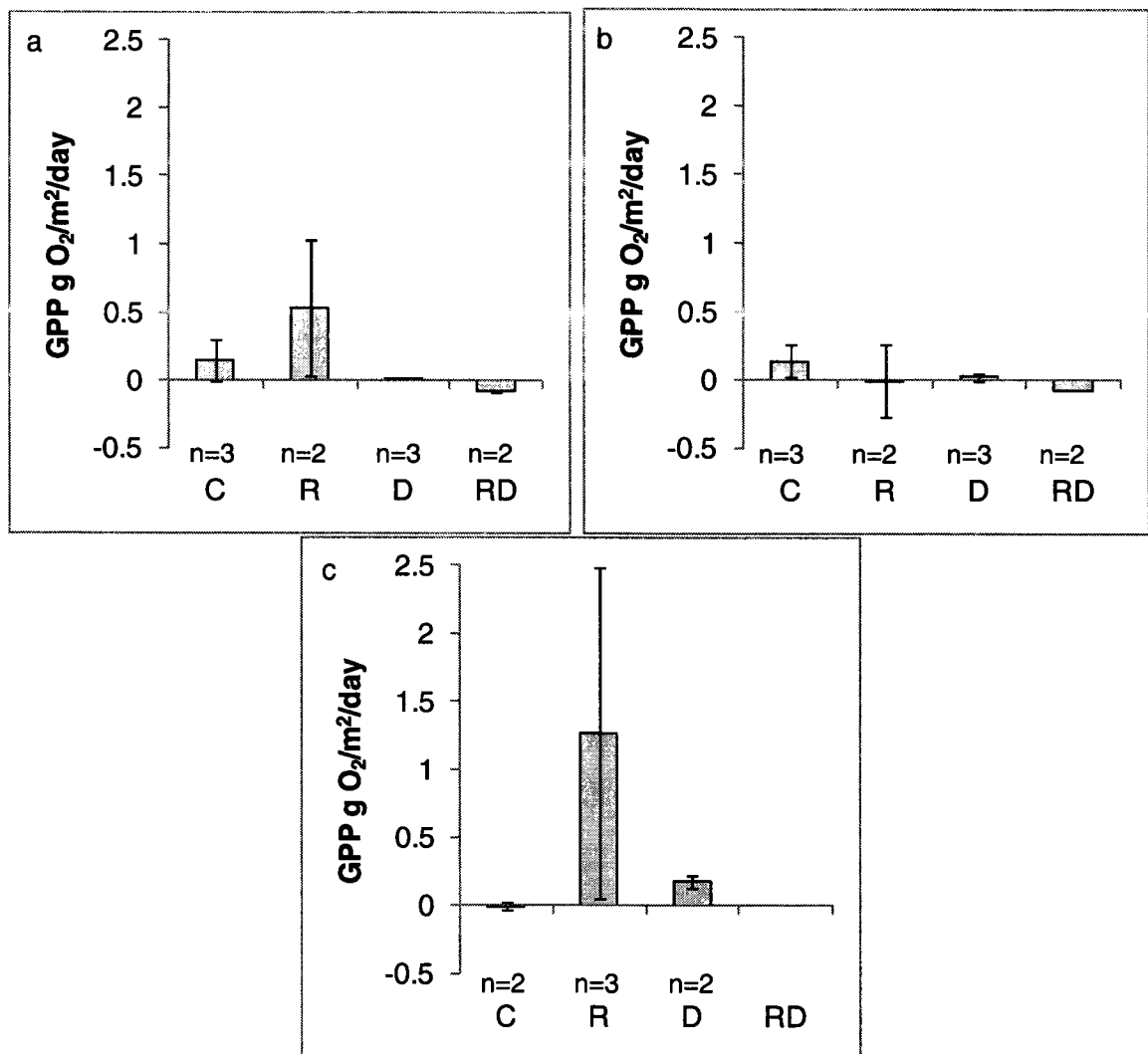


Figure 3.7. Differences between post-disturbance values and baseline measurements of GPP in the four types of experimental reaches six (a) twelve (b) and eighteen (c) weeks after initiating treatments. Columns show mean differences \pm 1 SE. Sample sizes are shown below each column.

disturbance frequency did not result in significant modifications of whole-stream metabolism, difficulty measuring whole-stream metabolism in these small, forested, high-gradient streams resulted in reduced sample sizes, and thus results of this study may generally underestimate effects of experimental treatments on ecosystem function. Furthermore, as noted above, experimenter error reduced experimental disturbance

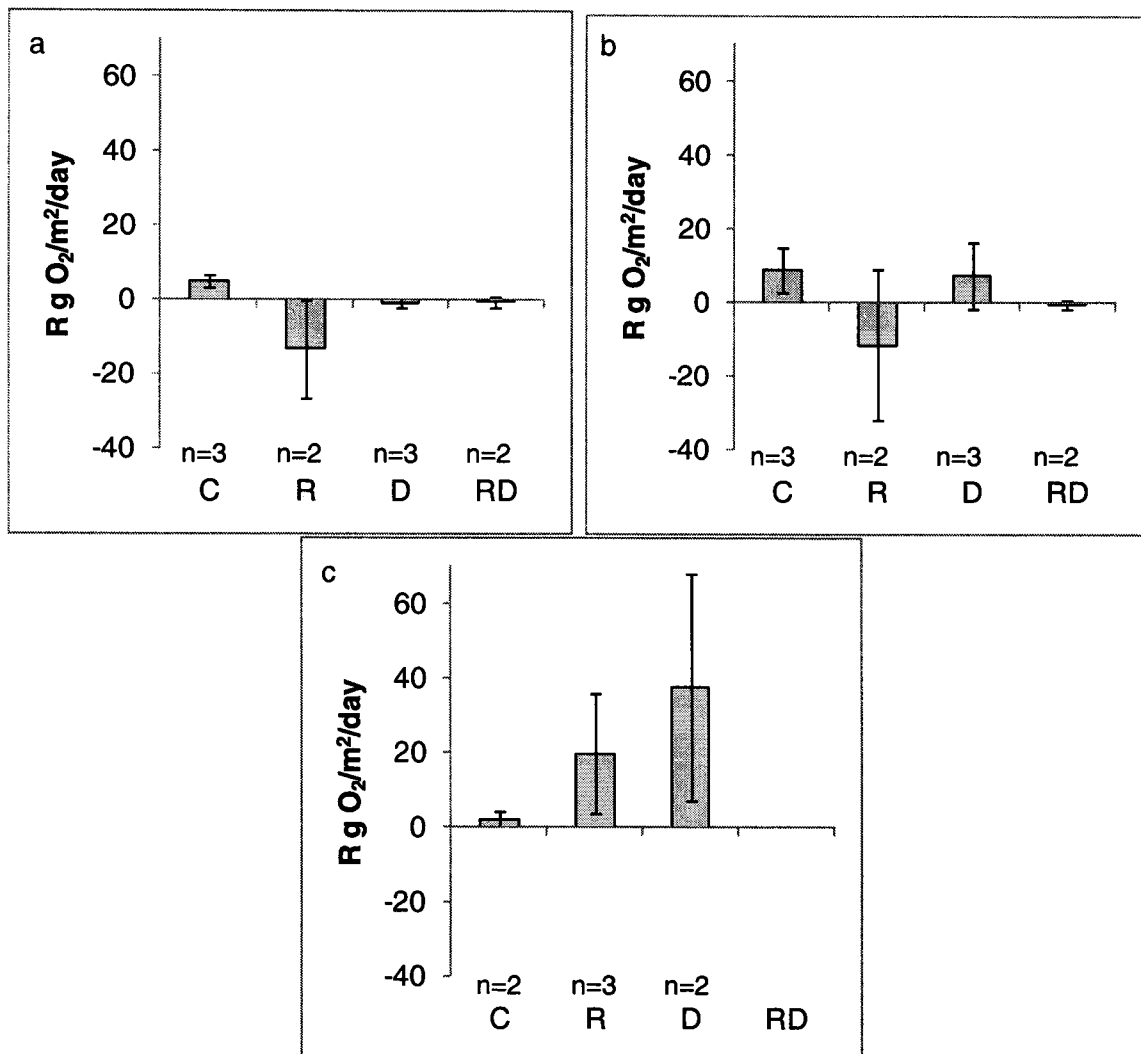


Figure 3.8. Differences between post-disturbance values and baseline measurements of R in the four types of experimental reaches six (a) twelve (b) and eighteen (c) weeks after initiating treatments. Columns show mean differences ± 1 SE. Sample sizes are shown below each column.

frequency in two of the eight high-disturbance-frequency experimental reaches during the final month of the experiment, which may have further reduced the impact of this treatment in the final sampling round.

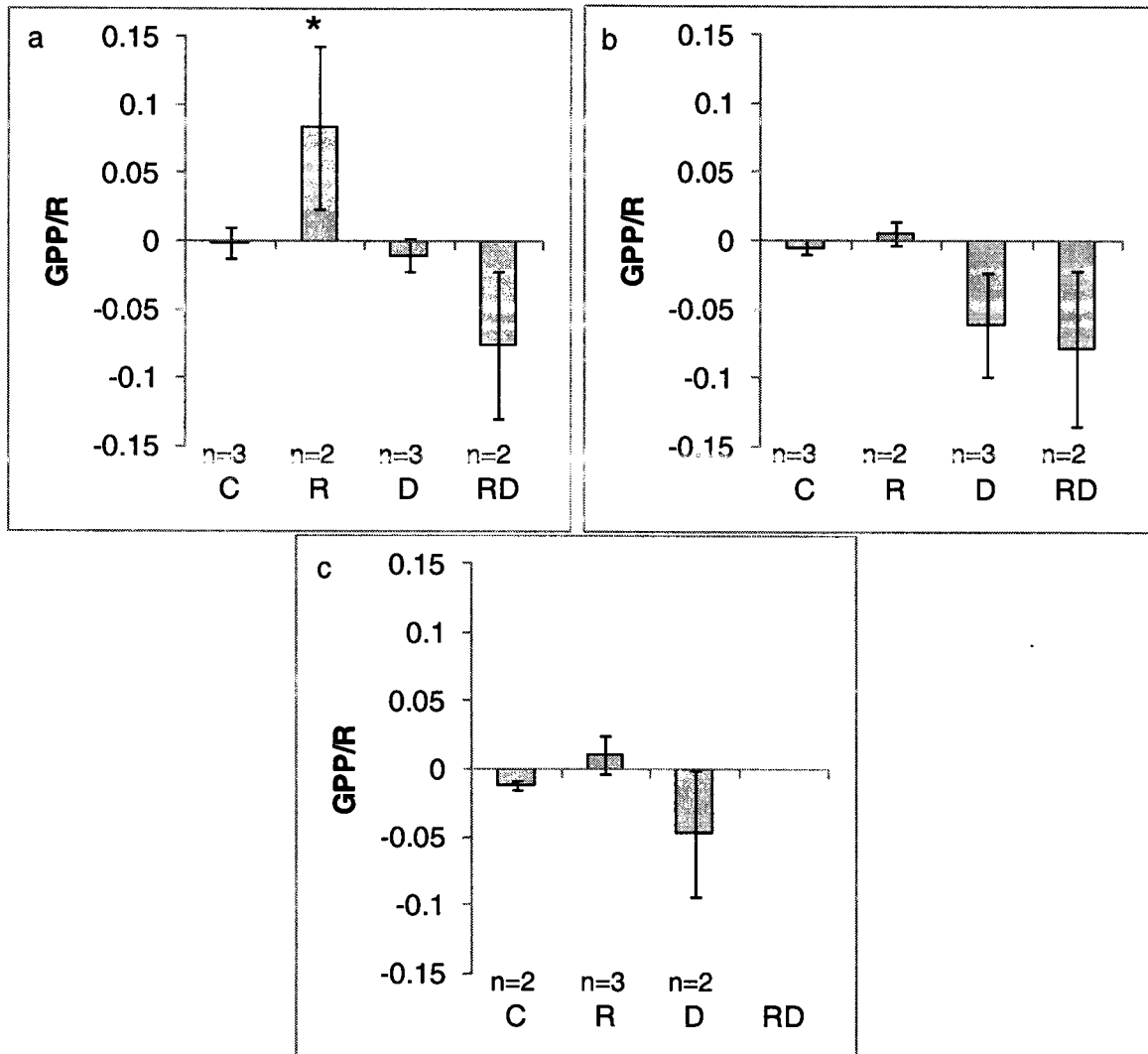


Figure 3.9. Differences between post-disturbance values and baseline measurements of GPP/R in the four types of experimental reaches six (a) twelve (b) and eighteen (c) weeks afterward. Columns show mean differences ± 1 SE. Sample sizes are shown below each column. Asterisk shows significant difference at the 95% confidence level in comparison with the control reaches using one-way ANOVA on log-transformed data with stream as a blocking factor and with Dunnett's comparisons.

Table 3.3a. Summarized mean differences between data collected during the first post-manipulation sampling round and baseline data for each type of experimental reach (C = control, R = rocks removed, D = disturbance, and RD = both treatments). Except for richness and rarefied richness, data were all log-transformed before taking differences. P-values are reported in parentheses for one-way and two-way ANOVA (treatments are abbreviated as RR. = rock removal treatment, Dist. = disturbance treatment, and Inter = treatment interaction). Note that asterisks indicate significance at the 95% confidence level.

	ANOVA p-val.	One-Way ANOVA				Two-Way ANOVA		
		C	R	D	RD	RR.	Dist.	Inter.
BOM	(0.60)	- 0.14	-0.19 (1.0)	-0.20 (1.0)	-0.27 (1.0)	(0.90)	(0.88)	(0.98)
Chlorophyll <i>a</i>	(0.27)	- 0.31	-1.8 (0.11)	-1.5 (0.24)	-1.7 (0.14)	(0.09)	(0.28)	(0.20)
Macroinvertebrate Abundance	(<0.001)	-1.0	-1.6 (0.01)*	-1.2 (0.30)	-1.6 (0.004)*	(0.001)*	(0.17)	(0.43)
Macroinvertebrate Family Richness	(0.03)	-8.0	-8.3 (1.0)	-5.0 (0.46)	-8.3 (1.0)	(0.31)	(0.38)	(0.38)
Rarefied Family Richness	(0.58)	-1.2	-1.7 (0.97)	-0.48 (0.94)	-1.4 (1.0)	(0.51)	(0.65)	(0.86)
GPP	(0.06)	0.05	1.2 (0.32)	0.28 (0.96)	-1.7 (0.15)	(0.47)	(0.13)	(0.03)*
R	(0.19)	0.82	-0.52 (0.19)	-0.11 (0.30)	-0.54 (0.18)	(0.10)	(0.21)	(0.34)
GPP/R	(0.01)	- 0.77	1.8 (0.02)*	0.39 (0.14)	-1.1 (0.86)	(0.23)	(0.48)	(0.01)*

Table 3.3b. Summarized mean differences between data collected during the second post-manipulation sampling round and baseline data. Data are reported as in Table 3.3a above.

	ANOVA p-val.	One-Way ANOVA				Two-Way ANOVA		
		C	R	D	RD	RR.	Dist.	Inter.
BOM	(0.23)	0.02	0.11 (0.99)	0.59 (0.48)	0.20 (0.96)	(0.66)	(0.33)	(0.47)
Chlorophyll <i>a</i>	(0.37)	0.40	0.57 (0.98)	-0.52 (0.36)	-0.52 (0.36)	(0.85)	(0.046)*	(0.85)
Macroinvertebrate Abundance	(0.01)	-0.43	-0.15 (0.36)	-0.45 (1.0)	-0.75 (0.28)	(0.94)	(0.047)*	(0.06)
Macroinvertebrate Family Richness	(0.02)	-6.8	-5.3 (0.58)	-3.8 (0.13)	-7.3 (0.97)	(0.33)	(0.62)	(0.03)*
Rarefied Family Richness	(0.03)	-2.4	-3.2 (0.32)	-2.1 (0.95)	-3.9 (0.046)*	(0.01)*	(0.55)	(0.26)
GPP	(0.16)	0.75	0.24 (0.96)	0.03 (0.87)	-3.1 (0.09)	(0.11)	(0.14)	(0.23)
R	(0.04)	1.15	0.59 (0.86)	1.1 (1.0)	-1.4 (0.09)	(0.06)	(0.26)	(0.18)
GPP/R	(0.58)	-0.40	-0.35 (1.0)	-1.0 (0.90)	-1.7 (0.69)	(0.77)	(0.38)	(0.74)

Table 3.3c. Summarized mean differences between data collected during the final sampling round and baseline data. Data are reported as in Table 3.3a above.

	ANOVA p-val.	One-Way ANOVA				Two-Way ANOVA		
		C	R	D	RD	RR.	Dist.	Inter.
BOM	(0.45)	1.3	0.77 (0.66)	0.91 (0.80)	1.1 (0.97)	(0.69)	(0.94)	(0.36)
Chlorophyll <i>a</i>	(0.18)	-0.27	-1.82 (0.04)*	-1.31 (0.17)	-1.14 (0.34)	(0.08)	(0.49)	(0.05)
Macroinvertebrate Abundance	(0.01)	-0.09	-0.30 (0.79)	-0.31 (0.77)	-0.96 (0.03)*	(0.06)	(0.053)	(0.30)
Macroinvertebrate Family Richness	(0.03)	-2.5	-1.8 (0.97)	0.25 (0.48)	-7.8 (0.09)	(0.04)*	(0.32)	(0.02)*
Rarefied Family Richness	(0.01)	-1.8	-0.80 (0.34)	-0.43 (0.15)	-2.3 (0.82)	(0.39)	(0.92)	(0.01)*
GPP	(0.07)	0.12	1.1 (0.22)	1.2 (0.25)	NA	(0.32)	(0.17)	NA
R	(0.17)	0.63	0.79 (0.93)	2.5 (0.13)	NA	(0.20)	(0.09)	NA
GPP/R	(0.09)	-0.51	0.33 (0.23)	-1.3 (0.31)	NA	(0.05)	(0.21)	NA

Despite these caveats, our results show that increased disturbance frequency has minimal impact on ecosystem structure and function in these forested streams, supporting the findings of Death and Zimmerman (2005). They found minimal impact of physical disturbance on periphyton biomass and macroinvertebrate diversity in New Zealand

forested streams. Primary production in these New Zealand streams was limited by light availability rather than rates of physical disturbance, and primary production in our streams may show similar light limitations.

Large streambed rocks appear to be very influential in maintaining stream ecosystem structure and function. The reduction in macroinvertebrate abundance associated with the removal of large stones during the first post-manipulation sampling round was also associated with increased GPP/R in undisturbed reaches from which large rocks had been removed. These concurrent effects suggest that primary production may have increased as a result of reduced top-down grazing pressure. Rock removal led to declines in macroinvertebrate rarefied family richness during the second post-manipulation sampling round as well as reductions in chlorophyll *a* and macroinvertebrate family richness in the final sampling round.

Large streambed particles may act as refugia and contribute to maintaining lotic ecosystem structure and function. Uehlinger (1991) described several mechanisms by which large stones support greater standing crops of periphyton: 1) large rocks protruding out of the stream are exposed to higher water velocities, which establish steeper nutrient gradients for epilithic biofilms, thereby more effectively providing nutrients, 2) large rocks are more stable and protect against abrasion during high flows, and 3) large rocks act as reservoirs of potential colonizers following floods.

Large stable stones may contribute to maintaining macroinvertebrate diversity by functioning as refugia for macroinvertebrates during high flows and/or by maintaining macroinvertebrate food resources. Matthaei et al. (2000) found that macroinvertebrates were concentrated on stable stones immediately following high flows, leading the authors

to propose that macroinvertebrates may actively seek out stable rocks during high flows and then subsequently recolonize the stream channel.

In this study, experimental treatments appeared to result in reductions in both chlorophyll *a* and macroinvertebrate diversity, after an initial time delay. While these two parameters may simply respond to disturbance in a similar manner, availability of epilithon (a macroinvertebrate food resource) may also control macroinvertebrate diversity. Death (2003) has proposed that the main effect of disturbance in New Zealand streams is removal of periphyton, which represents the base of the food web (the “productivity disturbance model”). Whether this holds true for North America has not been demonstrated-- fundamental differences in the ecological structure of streams between the two locations may change this relationship. Unlike in New Zealand, where obligate shredders are uncommon, litter generally represents the base of the food web in streams of the Northern Hemisphere (Death and Zimmermann 2005). Our study suggests that the productivity disturbance model may also be valid in the northeastern US. Macroinvertebrate diversity and chlorophyll *a* responded to rock removal in a similar fashion, while removal treatments had no significant effect on BOM availability. Further, results of our study support the idea that autochthonous carbon production is an important part of stream food webs, even in small streams where allochthonous organic matter inputs dominate (Peterson et al. 1993a, Finlay 2001). It is also notable that rock removal led to declines not only in macroinvertebrate family richness, but also in rarefied family richness. The latter is not sensitive to sample size and these results provide additional evidence for a mechanistic relationship between the availability of large rocks and the maintenance of diverse macroinvertebrate communities.

In addition to the importance of large rock refugia in streams, the results of this field experiment provide evidence that the combination of increased disturbance frequency and reduced numbers of refugium stones lead to greater losses of macroinvertebrate diversity and ecosystem function than does either treatment alone. Significant interactions between treatments were evident during all three post-manipulation sampling rounds, leading to reduced GPP and GPP/R during the first sampling round and reduced macroinvertebrate diversity in the last two sampling rounds. It is important to note that the four RD reaches that received the combination of both experimental treatments were located immediately downstream of the D reaches subjected to higher disturbance frequency, which were in turn located immediately downstream of R reaches subjected to removal of refugium stones. Being located farthest away from unmanipulated upstream sources of colonizers, these RD experimental reaches may have been more likely to exhibit reductions in ecosystem structure and function. However, as noted above, D reaches exhibited few significant effects in comparison to control reaches, and thus interactive effects were not likely amplified by the location of RD reaches. These documented interactive effects of increased disturbance frequency and reduced availability of large refugium stones suggest that in more frequently disturbed streams, stable refugia are indeed particularly important to maintaining stream ecosystem structure and function.

In evaluating the effect of experimental treatments over time during the three post-manipulation sampling rounds, it is notable that epilithon chlorophyll *a* and macroinvertebrate diversity parameters were not significantly altered until the second sampling round, 12 weeks following the initiation of experimental treatments.

Macroinvertebrates and epilithic algae may independently respond similarly to reduced availability of stable refugia and decline after an initial delay, or macroinvertebrate diversity may be dependent on the availability of periphyton, as proposed by Death (2003). Irrespective of the mechanism, it is important to note that altered stream channel substrate alone or in combination with modified disturbance regimes may result in changes in macroinvertebrate diversity that do not become apparent for several months.

Results of this study indicate that both structural and functional indicators are responsive to physical ecosystem disturbance in lotic systems. However, in small, high gradient, forested streams such as those involved in this experiment, measuring whole-stream metabolism may pose technical challenges and macroinvertebrate indicators may thus be more reliable to characterize the response to disturbance. Epilithon chlorophyll *a* may be a good proxy for primary production; a strong log linear relationship has been found between the two (Morin et al. 1999). Furthermore, epilithic algal abundance may drive macroinvertebrate diversity (Death 2003). On the other hand, since changes in near-bed hydraulics have been shown to alter biomass-specific productivity of epilithic algae (Cardinale et al. 2002), chlorophyll *a* may not reliably reflect changes in primary productivity following physical alterations to the streambed.

Although stream restoration projects frequently employ boulder placement strategies to enhance in-stream habitat heterogeneity, the effect of these practices on stream ecosystems has previously received little formal study. Results from this experiment highlight the importance of large refugium stones to maintaining lotic ecosystem structure and function. Further, this research indicates that the presence of

refugium stones is even more critical in streams exposed to increased frequency of physical disturbance.

CONCLUSION

The three studies presented in this dissertation document structural and functional responses of stream ecosystems to several different types of disturbances. This contributes to the small but growing body of research comparing the sensitivity of structural and functional indicators of lotic ecosystem health. A recent review by Sandin and Solimini (2009) concluded that, while structural metrics shouldn't be abandoned in favor of functional metrics, using functional indicators along with structural parameters may lead to a better assessment of lotic ecosystem health than using either structural or functional metrics alone.

The research presented in the previous three chapters provides additional information regarding which types of metrics are most sensitive to particular disturbances. These and other recent studies comparing the relative sensitivities of structural and functional metrics to environmental disturbance are a good first step towards being able to choose appropriate ecosystem metrics for different circumstances. However, to most effectively manage and monitor freshwater systems it is necessary to understand the mechanisms driving changes in ecosystem structure and function, and how these properties are linked.

As described in the first chapter, macroinvertebrate family richness was highly sensitive to acidification of small streams in the Czech Republic. Macroinvertebrate abundance, on the other hand, was not associated with pH; sensitive taxa (particularly Ephemeroptera) were replaced by tolerant taxa (particularly nemourid and leuctrid

stoneflies) in low pH streams. Whole-stream metabolism was also not significantly associated with pH, though GPP was strongly associated with ammonium concentration, which has also previously been identified as a driver of primary productivity. Thus, efforts monitoring impact of acidification on small streams would be advised to use measures of macroinvertebrate taxa richness and diversity, rather than whole-stream metabolism. Furthermore, the indication that macroinvertebrate diet at the family level shifts away from periphyton consumption at the most acidified study sites highlights the opportunity for future research to better elucidate the relationship between ecosystem structure and function in small acidified streams.

As described in the second chapter, sedimentation in and downstream of the Suncook River avulsion led to dramatic declines in macroinvertebrate abundance and whole-stream respiration, as well as changes in fish communities. High concentrations of suspended sediments are known to increase invertebrate drift, and sustained high levels of suspended sediment can deplete macroinvertebrate populations over time (Waters 1995). Deposited sediments can also lead to changes in macroinvertebrate communities, with EPT taxa replaced by burrowing chironomids and oligochaetes (Waters 1995). Fish communities are also influenced by sedimentation, as many fish avoid stream reaches with high concentrations of suspended sediments, and as deposited sediments block oxygen exchange in salmon redds and reduce riffle and pool habitat available for fish fry and adults, respectively (Waters 1995). Thus, community metrics are a good choice for monitoring impacts of sedimentation on stream ecosystems. While whole-stream respiration was depressed in and downstream of the Suncook River avulsed channel, further research is needed to clarify the mechanism for this response. While high levels of

suspended sediments would be expected to block sunlight to periphyton and depress GPP, primary productivity was not significantly reduced in or downstream of the new Suncook River channel.

Dewatering following the Suncook River avulsion also led to reductions in whole-stream respiration, and the mechanism for this effect is poorly understood as well. Additionally, dewatering resulted in changes to the fish community. On the other hand, changes in macroinvertebrate communities were harder to detect, and prior studies have found dewatering to have inconsistent effects on macroinvertebrate communities, suggesting that macroinvertebrate metrics may be a poor choice for studies assessing the impact of dewatering on stream ecosystems.

Finally, the last chapter highlighted the challenges of measuring whole-stream metabolism in small, high gradient, forested streams, where whole-stream metabolism may be overwhelmed by reaeration. In these systems, algae standing stocks may be a more reliable measure of primary production. Macroinvertebrate abundance and diversity were found to be sensitive to geomorphic manipulations in which large rocks were removed from experimental stream reaches, especially in combination with increased physical disturbance frequency. This study indicates that large rocks function as stable refugia for macroinvertebrates (and periphyton) during high flows. Thus, macroinvertebrate indicators would be a good choice for assessing impacts of altered geomorphology on small stream ecosystems. On the other hand, in larger, lower gradient rivers where whole-stream metabolism measurements are more reliable (and where macroinvertebrates may be more difficult to collect), these functional metrics may be more appropriate for monitoring impacts of altered geomorphology.

Generally, there may be situations that favor the use of functional over community metrics, such as stream sites with inaccessible habitats, large rivers, and studies involving comparisons among regions of different biogeography. At the same time, anthropogenic stressors can affect ecosystem processes through several mechanisms, which may result in complementary effects on functional metrics that cancel each other out. For example, agricultural streams are often exposed to elevated levels of turbidity (which depress GPP) along with increased nutrient concentrations and light exposure (which increase GPP). And while functional measures are comprised of a very limited number of parameters (decomposition rate, GPP, CR, and a few ways of combining GPP and CR), data from community studies are better suited for statistical ordination techniques that may more strongly indicate relationships with environmental variables. With public interest increasingly focusing on “ecosystem services”, the only way to assess ecosystem processes in streams is to measure them directly. In conclusion, to most effectively manage our freshwater resources, it is necessary to understand the mechanisms by which disturbances lead to changes in stream ecosystem structure and function, as well as the ways in which these factors are interconnected.

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APPENDIX A

IACUC APPROVAL LETTER

University of New Hampshire

Research Conduct and Compliance Services, Office of Sponsored Research
Service Building, 51 College Road, Durham, NH 03824-3585
Fax: 603-862-3564

29-Nov-2006

McDowell, William H
Natural Resources
James Hall
Durham, NH 03824

IACUC #: 061102

Project: Ecological impacts of sedimentation, dewatering, and new channel formation due to the May 15, 2006 avulsion of the Suncook River

Category: B

Approval Date: 17-Nov-2006

The Institutional Animal Care and Use Committee (IACUC) reviewed and approved the protocol submitted for this study under Category B on Page 5 of the Application for Review of Vertebrate Animal Use in Research or Instruction - *the study involves either no pain or potentially involves momentary, slight pain, discomfort or stress.*


Approval is granted for a period of three years from the approval date above. Continued approval throughout the three year period is contingent upon completion of annual reports on the use of animals. At the end of the three year approval period you may submit a new application and request for extension to continue this project. Requests for extension must be filed prior to the expiration of the original approval.

Please Note:

1. All cage, pen, or other animal identification records must include your IACUC # listed above.
2. Use of animals in research and instruction is approved contingent upon participation in the UNH Occupational Health Program for persons handling animals. Participation is mandatory for all principal investigators and their affiliated personnel, employees of the University and students alike. A Medical History Questionnaire accompanies this approval; please copy and distribute to all listed project staff who have not completed this form already. Completed questionnaires should be sent to Dr. Gladi Porsche, UNH Health Services.

If you have any questions, please contact either Roger Wells at 862-2726 or Julie Simpson at 862-2003.

For the IACUC,


Jessica A. Bolker, Ph.D.
Chair

cc: File